A MULTIPLE STABLE ISOTOPE STUDY OF STELLER SEA LIONS AND BOWHEAD WHALES: SIGNALS OF A CHANGING NORTHERN ENVIRONMENT

A

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ABSTRACT

The North Pacific and Arctic marine realm is currently experiencing dramatic environmental changes as a result of global climate change. Stable isotope analysis of western arctic bowhead whales (WABW, *Balaena mysticetus*) and Steller sea lions (SSL, *Eumetopias jubatus*) were conducted to examine the influence of these changes on life history characteristics (migration and foraging) of these marine mammals. WABW baleen plates were analyzed for their stable oxygen and hydrogen isotope composition ($\delta^{18}O$ and δD) and were compared to the $\delta^{18}O$ and δD in water and zooplankton prey along their seasonal migratory route. The $\delta^{18}O$ and δD varied along the baleen (8 to 18 ‰; -180 to -80 ‰, respectively) and corresponded to stable isotopic differences in zooplankton from the winter (Bering Sea) and summer (eastern Beaufort Sea) habitats of WABW. Baleen $\delta^{18}O$ and δD confirmed the seasonal annual migration of WABW and were subsequently compared to historical sea ice concentrations (SIC). This illustrated that WABW migration patterns appeared to have altered concomitant with changes in SIC. Years with a higher SIC (colder climate regimes) correlated with the largest difference in δD between winter and summer in WABW baleen during the period from 1972 to 1988. For a similar time period (1955 to 2000), the feeding ecology of SSL was also examined by analyzing the stable carbon and nitrogen isotope compositions ($\delta^{13}C$ and $\delta^{15}N$, respectively) of archived SSL bone and tooth collagen. Both $\delta^{15}N$ and $\delta^{13}C$ varied greatly with location and sample year (14.6 to 20.5 ‰; - 16.7 to -11.8 ‰, respectively), with a significant change in $\delta^{13}C$ observed around the 1976 regime shift. Bottom-up processes may have limited growth of SSL populations throughout this region over time, with

animals focusing their foraging on offshore regions to mitigate this environmental change. Stable isotope analyses of historical samples of WABW (baleen) and SSL (bone and tooth collagen) both illustrated that recent environmental changes influenced the ecology (migration and feeding) of these marine mammals in the recent past.

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LIST OF ABBREVIATIONS

ASIF – Alaska Stable Isotope Facility

CO – Carbon Monoxide

CO_2 – Carbon Dioxide

EA – Elemental Analyzer

H_2 – Hydrogen

HCl – Hydrochloric Acid

IRMS – Isotope Ratio Mass Spectrometer

N_2 – Atmospheric Nitrogen

NIST – National Institute of Standards and Technology

NOAA - National Oceanic Atmospheric Administration

NMFS – National Marine Fisheries Service

NRC – National Research Council

SD - Standard Deviation

SIC – Sea Ice Concentration

SMOW – Standard Mean Ocean Water

SSL – Steller Sea Lion

TC/EA – Temperature conversion elemental analyzer

VPDB – Vienna PeeDee Belemnite

VSMOW – Vienna Standard Mean Ocean Water

WABW – Western Arctic Bowhead Whale

10^{th}s – Sea Ice Concentration Units

‰ – parts per thousand; per mil

$\delta^{13}C$ – Stable Isotope Ratio of Carbon

δD – Deuterium; Stable Isotope Ratio of Hydrogen

$\delta^{15}N$ – Stable Isotope Ratio of Nitrogen

$\delta^{18}O$ – Stable Isotope Ratio of Oxygen

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CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION

1.11 Background

Areas of the Arctic and sub-Arctic are experiencing some of the most rapid and severe climate change on earth (IPCC 2001; Karl and Trenberth 2003; ACIA 2004). In the next century, it is predicted that climate change will accelerate to an even greater degree, further contributing to major ecological shifts in the Arctic (ACIA 2004). There will likely continue to be changes in temperature, precipitation, sea ice extent, and sea level rise, among other variables (IPCC 2001). The effects these extreme transformations will have on the life history patterns of marine mammals are of imminent concern to mitigate species population declines and extinctions, as well as the detrimental effects on commercial harvest and subsistence communities (ACIA 2004). The high latitudes of the arctic and sub-arctic Pacific are particularly sensitive to climate change (Comiso 2003) and are liable to be regions where the early effects of global climate change on animal behavior will become most noticeable. While some studies of shifts in arctic flora and fauna have occurred, they have been largely focused on the terrestrial realm (Hobson 1999; Hobson *et al.* 1999; Loreau *et al.* 2001), rather than marine environments. To assist in filling this research gap, I chose to examine the influence of recent changing environmental conditions on the migration and foraging patterns of two predominant marine mammal species in the region: a commercially and socially integral

pinniped, the Steller sea lion (SSL, *Eumetopias jubatus*), as well as the highly migratory and ice-dependent western arctic bowhead whale (WABW, *Balaena mysticetus*).

Both of these species are proposed to have been influenced by, amongst a suite of competing hypotheses, recent environmental change. For instance, WABWs may be shifting their current over-wintering habitat due to the effects of both decreased productivity in the Bering Sea (Schell 2000) and large warming anomalies in annual sea ice extent (Gates 1993; ACIA 2004). The planktonivorous WABWs, which migrate between wintering areas in the Bering Sea and summer regions in the eastern Beaufort Sea (Braham 1984; Schell *et al.* 1988; Moore and Reeves 1993), likely are particularly susceptible to changes in sea ice patterns and primary productivity in the Arctic and sub-Arctic. Simultaneously, pinnipeds in the North Pacific Ocean and southern Bering Sea have declined substantially over the past few decades (National Research Council 1996, 2002). SSL in particular, with the bulk of the species residing in Alaskan waters of the North Pacific, have shown the most dramatic population reduction in recent decades (York 1994; Merrick *et al.* 1997; Loughlin 2002). Collectively, these changes are among the most severe and perplexing megafaunal perturbations in recent times. In order to examine these major alterations from a historical perspective, it is important to choose a scientific methodology that can effectively recreate past migratory and foraging patterns. For this purpose, the analysis of naturally occurring stable isotope signatures in historical samples of WABW and SSL is a valuable way to enhance understanding of these patterns from an ecological context.

1.12 Stable isotope analyses

The analysis of stable isotopes is a powerful technique to decipher changes in migration patterns (Burton and Koch 1999; Hobson 1999; Lee *et al.* 2005) and diet (Deniro and Epstein 1978, 1981; Dunton *et al.* 1989; Schell *et al.* 1989; Hobson and Welch 1992; Hobson *et al.* 1997; Kelly 2000; Hirons *et al.* 2001). Animals that regularly move across naturally occurring isotopic gradients during seasonal migrations can acquire distinct isotopic signatures along their migratory path and record them in their tissues (Deniro and Epstein 1978; Peterson and Fry 1987; Hobson and Welch 1992; Burton and Koch 1999; Hobson 1999; Webster *et al.* 2002). Soft tissues, such as blood and fat, are constantly regenerating; this turnover continuously alters their stable isotopic composition. However, some tissues are laid down incrementally (e.g., teeth, hair, nails, and feathers) and provide an isotopic record, or biological archive, of an animal's migratory and feeding history (Peterson and Fry 1987; Schell *et al.* 1988; Koch *et al.* 1989; Schell *et al.* 1989; Hobson and Welch 1992; Michener and Schell 1994; Hobson 1999; Hirons 2001). In the case of WABW, this isotopic record is present as keratinous tissue, laid down incrementally in the form of baleen plates. For SSL, collagenous hard tissues such as bone and teeth record diet in a composite and temporally incremental fashion, respectively.

Stable carbon and nitrogen isotope ($\delta^{13}C$ and $\delta^{15}N$, respectively) compositions of animal tissues have also been used to examine foraging patterns. Differences in $\delta^{13}C$ and $\delta^{15}N$ at the base of the food web are passed on to higher trophic levels with small, consistent offsets (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Minagawa and Wada 1984; Kelly 2000). They have also served as natural labels in prior studies of

marine mammal and bird foraging ecology (Schoeninger and DeNiro 1984; Wada *et al.* 1987). While some studies have served as important baselines for deciphering the subsequent variations in feeding patterns and habitat selection of marine mammals specifically, including the SSL (Hobson *et al.* 1997; Burton and Koch 1999; Hirons *et al.* 2001; Kelly 2000), it has become important to increase the spatial and temporal resolution of the isotopic record throughout the North Pacific to generate a comprehensive picture of changes in SSL foraging ecology. To achieve this enhanced resolution, isotopic analyses of teeth (Hobson and Sease 1998) are useful to both expand the current dataset and construct a time series of SSL populations throughout their range.

The $\delta^{13}C$ and $\delta^{15}N$ analyses of keratin along baleen plates have also previously afforded insight into bowhead whale feeding ecology (Schell *et al.* 1988, 1989; Dunton *et al.* 1989; Lowry, 1993; Michener and Schell, 1994; Lee *et al.* 2005). The stable oxygen and hydrogen isotope compositions ($\delta^{18}O$ and δD, respectively) of organic compounds laid down incrementally in animal tissues (e.g., baleen plates or otoliths) could also serve as additional valuable tracers of migratory behavior (e.g., Whitledge *et al.* In press). There are potentially large isotopic gradients present between the waters of the Bering and Beaufort Seas (Lee 2000; Bowen *et al.* 2005). Given the relatively novel nature of examining $\delta^{18}O$ and δD of animal tissues in marine systems (Bowen *et al.* 2005; Knoche *et al.* In review), it is important to concurrently identify baseline $\delta^{18}O$ and δD signatures in the water and prey components in the ecosystem of the WABW. This is necessary in order to conduct a fine-scale examination of their migratory patterns, in much the same way that others did when

embarking upon the analysis of $\delta^{13}C$ and $\delta^{15}N$ in WABW baleen (Schell *et al.* 1988; Schell 1998; Schell *et al.* 1998).

1.13 Scope of study

This study aims to identify the historical influences and responses of marine mammals to environmental changes in the North Pacific, Bering Sea, and Arctic Ocean. A major goal of this research is to identify the temporal and spatial changes in foraging patterns of SSL using collagenous hard tissues. In this study, tooth samples were utilized to supplement $\delta^{13}C$ and $\delta^{15}N$ data from bones to obtain a temporal resolution dataset covering the period before and after the decline of the SSL (~1966-1998) and over the entirety of their range (Russia to California) (York 1994; Merrick *et al.* 1997; Loughlin 2002). Changes in $\delta^{13}C$ and $\delta^{15}N$ in both teeth and bones were examined in reference to the major regime shift (1976) during this decline period (Francis and Hare 1994; Steele 1998; Hare and Mantua 2000).

Another major goal of this study is to identify the utility of δD and $\delta^{18}O$ analyses in WABW baleen to enhance understanding of their migratory patterns. The water and major dietary components of WABWs were examined using these same isotopes to determine trends in δD and $\delta^{18}O$ within the marine ecosystem. Further, these WABW migratory patterns established from δD and $\delta^{18}O$ were analyzed in the context of historical sea ice concentration data for the Bering Sea region to determine the effects of environmental change on habitat selection of WABWs. The results of this study will aid

in the understanding of basic biology, conservation, and management of these integral species in relation to their environment.

Chapter 2 characterizes the historical feeding ecology of SSL through an examination of the $\delta^{13}C$ and $\delta^{15}N$ signatures preserved in SSL teeth and bone. The period of investigation, 1955 to 2001, straddles both the recent marked decline in SSL as well as the 1976 regime shift. Teeth and bone samples from SSL throughout their range were analyzed to compare and evaluate the effects of sex and tissue type on the temporal and spatial isotopic patterns. These data were also used to examine a marked shift that occurred concomitant with the start of the decline and in relation to the 1976 regime shift.

Chapter 3 examines the environmental patterns and migratory behavior of WABW traveling between the Bering and Beaufort Sea. The δD and $\delta^{18}O$ of water, zooplankton, and WABW baleen were analyzed to compare and evaluate the utility of δD and $\delta^{18}O$ for examining whale migrations, as well as general patterns of these two stable isotope tracers passing through the arctic and sub-arctic marine ecosystem.

Chapter 4 examines the relationship of the migratory patterns of the WABW, using δD and $\delta^{18}O$ analyses of WABW baleen, in the context of changing climate regimes and sea ice concentrations. Sea ice concentrations were temporally correlated with stable isotopic trends in WABW baleen to evaluate the effects of climate regimes and physical forcing on habitat selection of the bowheads.

Chapter 5 reports the general conclusions of the results of the previous chapters, and their utility in identifying patterns in marine mammal foraging and migration relevant

to the environments in the North Pacific and Arctic Oceans. General conclusions and the impact of the research on future studies are included in closure.

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CHAPTER 2

THE HISTORICAL ECOLOGY OF STELLER SEA LIONS: AN ISOTOPIC STUDY OF MAMMALIAN RESPONSES TO A CHANGING ENVIRONMENT[1]

2.1 ABSTRACT

Defining a cause of the recent rapid decline of pinniped populations in the Bering Sea and the Gulf of Alaska is a topic of controversy. In spite of apparent top-down pressure from fisheries in these regions, no definitive links between bottom-up processes and marine mammal declines have been established. In order to determine the influence of changes in pinniped foraging on this decline, stable isotope (C and N) data were used to reconstruct the ecology of Steller sea lions (SSL-*Eumetopias jubatus*). Analyses of bone and tooth collagen show variations in the stable carbon isotope composition ($\delta^{13}C$) of SSL populations, suggesting shifts in diet and trophic diversity that are correlated with the population decline. No systematic change was observed in the nitrogen isotope composition ($\delta^{15}N$) throughout the study period. Both isotopes vary greatly with location and sample year ($\delta^{15}N$ = 14.6 to 20.5 ‰; $\delta^{13}C$ = - 16.7 to -11.8 ‰), with a significant change in $\delta^{13}C$ value in bones at the point of a major regime shift period (~1976). Bottom-up processes may have influenced SSL populations throughout the North Pacific region over time, with animals focusing their foraging on more offshore regions to mitigate this shift.

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[1] DEHART, P.A.P., V.K. STEGALL, B.P. FINNEY, P.L. KOCH AND M.J. WOOLLER. The historical ecology of Steller sea lions: An isotopic study of mammalian responses to a changing environment. Prepared for submission to Marine Mammal Science.

Keywords: Stable isotopes; *Eumetopias jubatus*; Steller sea lion; foraging ecology; population decline

2.2 INTRODUCTION

2.21 North Pacific populations

Marine mammal populations in the North Pacific Ocean and southern Bering Sea have declined substantially over the past few decades (National Research Council 1996). Collectively, these declines are among the most severe and perplexing megafaunal collapses in recent times. Steller sea lions (SSL, *Eumetopias jubatus*), which range from California to the Kuril Islands in Russia, with the bulk of the species residing in Alaskan waters, have shown the most dramatic population reduction in recent times (York 1994; Merrick *et al.* 1997; Loughlin 2002).

While the early historical ecology and biogeography of SSL populations is poorly known, large numbers of these animals inhabited the western Gulf of Alaska and Aleutian Islands in the mid-20th century. SSL numbers in this region declined sharply in the early to mid-1980s, and by the late 1980s were less than 20 % of the initially well-documented levels (Merrick *et al.* 1987; Loughlin *et al.* 1992; York 1994; Loughlin 2002). As a result of this alarming diminution, this species is now listed as either endangered or threatened throughout its range (Call and Loughlin 2005). To account for this decline, a suite of multiple competing hypotheses has been proposed to explain the forces driving this massive population shift. These hypotheses have included

examinations of competition with fisheries operations (Merrick *et al.* 1997), physiological effects of nutritional limitation to body condition (Rosen and Trites 2000; Andrews *et al.* 2002; Winship and Trites 2003), and most recently, connections with top-down driven processes such as changes in killer whale feeding strategies (Springer *et al.* 2003).

A review of the SSL decline by the U.S. National Research Council concluded that top-down forcing posed the greatest threat to the current reduced populations, but that the lack of baseline data on the biology of earlier populations precludes assessment of the role of bottom-up factors in the initial decline of the species (National Research Council 2002). Additionally, while it has been suggested that altered food web dynamics may have provided the initial trigger causing such a large shift in population (Springer *et al.* 2003), recent studies attempting to determine whether SSL diets shifted over the decline period (Schell *et al.* 1998; Hirons 2001) have been limited in spatial and temporal scope and therefore are insufficient to fully address this question. One of the most intriguing temporal features that occurred during the SSL decline relates to what has become known as a "regime shift" that may have influenced environmental conditions and thus impacted SSL populations.

2.22 Regime shift

After over a decade of research into past climate patterns, a climatic regime shift is now accepted to have taken place in the North Pacific Ocean at the end of 1976 (Francis and Hare 1994; Steele 1998; Hare and Mantua 2000). Regime shifts are large

scale climatic and oceanographic alterations that affect the biology of multiple species, populations, communities, and ecosystems on a decadal to multi-decadal scale (Steele 1998). Climate-driven regime shifts, such as those identified in the north-east Pacific, can cause major reorganizations of ecological relationships over vast oceanic regions, and produce cascading effects throughout the food web up to higher level predators (Francis and Hare 1994). The consequences of the 1976 shift were complex and far-reaching on the greater marine ecosystems of the North Pacific (Francis and Hare 1994; Steele 1998; Hare and Mantua 2000). It is clear from an examination of the climatic and biological record that an additional shift transpired to a lesser extent in 1989, which also overlaps with the continued decline of SSL in the North Pacific (Steele 1998; Hare and Mantua 2000).

Multiple lines of evidence need to be closely monitored, including the biological and climatic details (e.g., profiles of fish and invertebrate distribution and abundance, trends and changes in temperatures at the sea surface and depth) in the North Pacific and Bering Sea ecosystems to identify the likely impact of future regime shifts (Steele 1998; Hare and Mantua 2000). An understanding of ocean systems is essential for ecosystem management. In particular, the benefits of comparative and observational perspectives of a "historical-descriptive" approach, such as stable isotope analysis, have been touted as essential to obtaining insight into the broad impacts of regime shifts, particularly in the North Pacific Ocean (Francis and Hare 1994). Understanding biological patterns on both temporal and spatial levels allows for a standardization of scale in an otherwise difficult

analysis of environmental change. The analysis of stable isotopes in animal tissues is an efficient method for such studies.

2.23 Stable isotope analyses

Stable isotope analysis can provide a means of studying past animal diets. Because of differences in water column stratification, carbon cycling and growth rate, primary producers in nearshore/benthic systems tend to have higher carbon isotope ($\delta^{13}C$) values than those in offshore/pelagic systems (Michener and Schell 1994; Francis *et al.* 1998; Schell *et al.* 1998). These $\delta^{13}C$ differences at the base of the food web are passed on to higher trophic levels with small, consistent offsets (DeNiro and Epstein 1978; Kelly 2000), and have served as natural labels in prior studies of marine mammal and bird foraging ecology (Schoeninger and DeNiro 1984; Wada *et al.* 1987; Schell *et al.* 1988; Schell 1998). Among marine mammals, the $\delta^{13}C$ values differ between nearshore and offshore foragers, with offshore feeders such as the northern fur seal (*Callorhinus ursinus*) having more negative values than nearshore foragers (e.g., harbor seal, *Phoca vitulina*) (Burton and Koch 1999; Burton *et al.* 2001; Hirons *et al.* 2001).

In another approach, Schell (2000) suggested that in marine mammals, a substantial temporal decrease in the $\delta^{13}C$ with no change in the $\delta^{15}N$ may correspond to a decrease in the level of carbon fixation in the habitat and be indicative of changes in primary productivity due to a long-term change in climate regime. Nitrogen isotope ($\delta^{15}N$) values vary spatially due to oceanographic differences, particularly across the Bering Sea (Schell *et al.* 1998), but these differences are not consistently related to

onshore/offshore location. Equally important for this study is the marked increase in the $\delta^{15}N$ evident with increasing trophic level in many ecosystems (DeNiro and Epstein 1981; Minagawa and Wada 1984; Kelly 2000).

Although the two previous stable isotopic studies of SSL in Alaskan waters (Hobson *et al.* 1997; Hirons *et al.* 2001) serve as valuable starting points and sources of comparative data for our analysis, the data sets are too limited to assess both spatial and temporal patterns associated with the SSL decline. We thus sought samples representative of the whole expanse of this species' range, and extending temporally from prior to their precipitous decline. We restricted our analyses to include only animals aged 2.5 years or older, to assure the stable isotope values obtained from the tissue (collagen) of the animals reflected only weaned individuals (Minigawa and Wada 1984; Hobson *et al.* 1996; Hobson and Sease 1998). Teeth were chosen both to expand the current established dataset, which was based primarily on bone samples, and to construct a time series of animals throughout their range.

2.24 Steller sea lions

Steller sea lions spend much of their year foraging over the continental shelf and in the offshore waters of the southern Bering Sea (Merrick *et al.* 1997; Loughlin 2002). Male SSL are larger in size and have greater nutritional requirements than female SSL, so are typically independent and highly migratory at sea. Throughout the breeding season, males can eat very little while on the territory (Loughlin 2002). Females, on the other hand, stay close to their home range and feeding source (Sinclair and Zeppelin 2002;

Milette and Trites 2003), and are therefore liable to be a more accurate indicator of local environmental patterns.

To interpret stable isotope data, it is necessary to identify the characteristics of likely SSL foraging components. The diets of SSL in Alaska waters are currently dominated by larger fish, such as gadids (e.g., walleye pollock, *Theragra chalcogramma*; Pacific cod, *Gadus macrocephalus*), Atka mackerel (*Pleurogrammus monopterygius*), and salmon (*Oncorhyncus* spp.), with lesser amounts of small schooling fish (e.g., capelin, *Mallotus villosus*; herring, *Clupea h. pallasi*) and cephalopods (Merrick *et al.* 1997). Studies of SSL diets prior to their decline suggest they consumed more small schooling fish (Mathisen *et al.* 1962; Fiscus and Baines 1966; Pitcher 1981; Merrick *et al.* 1997). Thus, one bottom-up hypothesis for the SSL decline is a drop in the availability of small fish, due to oceanographic features or depletion by fisheries. Merrick *et al.* (1997) offered an alternative bottom-up hypothesis. They compared SSL diets in regions with stable versus declining populations and noted a correlation between steep rates of population decline and low dietary diversity, suggesting that SSL could require a variety of prey to buffer changes in availability of individual prey species. An alternative explanation for this correlation is that in areas of steep population decline, SSL numbers are now so low that populations specialize on high-rank prey (National Research Council 2002). Without data on historical diet trends, it is impossible to determine if the current situation is the norm or unusual for this species.

2.25 Hypotheses

Before using stable isotope measurements of historical samples of SSL, we wished to begin with an assessment of the applicability of our particular dataset, and determined the inherent characteristics of our sample selection. We aimed to test whether differences in stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) were significantly influenced by sample type (bone versus tooth). Although we limited any effect of weaning by selecting growth layers in teeth greater than three years, we wished to test whether ontogenetic trends were evident. If the data are representative of individual behavioral patterns, rather than a consistent ontogenetic influence, we expected to see no systematic changes in either $\delta^{13}C$ or $\delta^{15}N$ over growth layers from different animals. We also hypothesized that there will be differences in isotopic values between males and females. Due to the larger size, nutritional requirements, and known movement patterns of male SSL, they could exhibit less cohesive and consistent trends in their $\delta^{13}C$ and $\delta^{15}N$ values in both temporal and spatial scales. If this difference exists, then it would be necessary to focus on female samples for further analyses, given that they are likely more indicative of a specific geographic region, simplifying the examination of spatial patterns. If no difference is observed between the sexes, then males and female samples will be grouped together for general temporal and spatial analyses. Spatial differences in SSL diet, as displayed in changes of the mean and variance in $\delta^{13}C$ and $\delta^{15}N$, are expected given the large geographic region of our sample set. If there are observed systematic differences in the $\delta^{15}N$ with location, this suggests that animals from a particular region may be feeding on prey representing a different trophic level. Changes in $\delta^{13}C$, however, may also be

indicative of fine-scale oceanographic and circulation patterns specific to that sample region. If SSL diets are consistent with location, then there may be little difference in $\delta^{13}C$ and $\delta^{15}N$, and the forces acting on the entire study region are likely similar.

To examine the feeding ecology of SSL during the decline using stable isotopes, we tested a series of competing hypotheses. If SSL systematically changed the trophic level at which they were feeding during the decline period, we would expect to see a marked change in $\delta^{15}N$ recorded in their teeth and bones (i.e. ~3 ‰ for a single trophic level). This may also be expected to be accompanied by smaller (~1 ‰) change in $\delta^{13}C$ if a single trophic level difference existed. A shift in diet selectivity (e.g., change in fish species type or size) could also cause both isotopes' values to shift markedly at the start of the SSL decline. A change in $\delta^{13}C$ and/or $\delta^{15}N$ could also mark changes in feeding location over time. For instance, a shift to lower $\delta^{13}C$ values with time could indicate that SSL were searching for prey in more offshore regions. Such a temporal change in $\delta^{13}C$ at a specific point in time, such as the aforementioned regime shift, with no corresponding change in $\delta^{15}N$ could be driven by altered primary productivity in SSL habitats, as previously suggested by Schell (2000). It is the interplay of the two isotopes that should elucidate the patterns of diminution in the SSL. Any and all differences in $\delta^{13}C$ and $\delta^{15}N$ of SSL will be put in perspective of previously established prey and lower trophic level values (Kurle and Worthy 2001) as well as previous SSL stable isotope data. If the $\delta^{13}C$ and $\delta^{15}N$ are consistent throughout the study period, this would not necessarily imply that the primary food sources remained constant throughout the study period, but rather prey type within the same trophic level (i.e., clupeids and gadids, displaying

overlapping $\delta^{13}C$ and $\delta^{15}N$ with large variance; Merrick *et al.* 1987; Hobson *et al.* 1997) may indeed have changed, but could not be detected using stable isotope analyses (Schell 1998). An alternative, however, is that if SSL feeding ecology did not change significantly over time, it would thus be unlikely that the precipitous decline was due to bottom-up effects but rather was driven by top-down effects, such as increased predation on the population by killer whales (e.g., Springer *et al.* 2003).

2.3 MATERIALS AND METHODS

2.31 Sample collection

Bone samples from adult male (n = 41) and female (n = 81) SSL (ranging in age from 3 to 17 years) were obtained from the archived collection at the National Marine Mammal Laboratory (Seattle, WA). Between 2.0-3.0 g of bone was sectioned from the left mandible (Figure 2.1d). Animals ranged from southeastern Russia to southern California and represented the years between 1955 and 2001 (Figure 2.2). For temporal data analysis, bone samples were assigned the year of death for the animal. Tooth samples from adult female SSL (ranging in age from 3.5 to 31 years) (n = 74) were obtained from the archived captured and necropsied animals from the Alaska Department of Fish and Game (Anchorage, AK). Longitudinal tooth segments (~ 1.5 mm wide) (Figure 2.1a-c) from each animal were sampled to represent 3-5 year classes (beyond the first 2.5 years of life- to eliminate any weaning isotopic signal) using a Dremmel tool. Tooth samples represented a total of 194 tooth segments from all 74 animals (26

segments were not included in the analyses, as they represented age classes below 2.5 years).

For ontogenetic analysis, tooth segments were divided into outer, middle, and inner layer groups, representing material established earliest, in the middle, and towards the end of life of the animals, respectively. These segments were assigned to the middle year of the group of years represented by each growth band, to aid a structured temporal analysis. The latest possible date for each segment was used for data analysis and display (e.g., the innermost segment of a tooth from an animal killed in 1972 would be assigned the year 1972). Including the 122 mandible bone segments, a total of 316 samples (from 196 animals) were used for data analysis and comparison. Given the current developments and literature with respect to geographic separation of "western" vs. "eastern" populations, samples were selected first along a longitudinal gradient instead of a distinguished single-point separation. For further geographic comparison, samples were grouped into seven regions from west to east (listed in Table 2.2), according to clumping of available samples and previously established major rookery distributions (Trites and Larkin 1996).

2.32 Collagen extraction

All samples (bone and teeth) underwent collagen extraction following the protocol established by Matheus (1997). Samples were initially cleaned and prepared over two days by alternating rinsing in double-distilled water with soaking in chloroform a minimum of two times at 8 hours each. Samples were then air-dried under a fume hood

and rinsed well with double-distilled, ultra-pure water. The samples were subsequently demineralized in a mildly acidic double-distilled water/6N HCl mixture (approx. 5ml H_2O/1.5ml HCl) at 5°C for 4-7 days with daily acid exchange/recharge. The remaining translucent bone and tooth pieces were then gelatinized in low pH (~3-4) water at 55°C for approximately 24 hours on a vortex evaporator (LabConco Model # 4322000) at a speed of approximately 5.5 rotations per second. The remaining supernatant was then filtered with a 50 mm syringe through a 0.45μ pore size glass disk (Millipore), and the resultant sample was super-cooled at -70°C before being lyophilized.

2.33 Stable isotope analysis

A sub-sample of between 0.2-0.4 mg of collagen was analyzed for its $\delta^{15}N$, $\delta^{13}C$, and elemental compositions (% C and % N). All the sub-sample aliquots from each animal were analyzed using an elemental analyzer coupled to a Thermo Finnigan Delta^{plus} XP isotope ratio mass spectrometer. The values obtained are expressed in standard delta (δ) notation, as parts per thousand (‰). Ratios were expressed as:

$\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard})-1] \times 1{,}000$

where R_{sample} and $R_{standard}$ are the ratios of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for the sample and standard, respectively. Values are all expressed relative to atmospheric N_2 (At-air) for nitrogen and Vienna PeeDee Belemnite (V-PDB) for carbon. Peptone was used as a chemical reference material to assess analytical precision, with instrument reproducibility for both $\delta^{13}C$ and $\delta^{15}N$ at ± 0.2 ‰. Samples were run in duplicate and repeated if the difference

between replicates was greater than 0.5 ‰. Analytical error for all samples was estimated to be 0.3 ‰ and 0.1 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

2.34 Statistical analysis

Data are expressed throughout as mean ± 1 standard deviation (SD). We used two-way ANOVAs to compare sex, tissue type, and location both throughout the whole study period and temporally separated before and after 1976. Two-way ANOVAs were also used to compare bone $\delta^{13}C$ and $\delta^{15}N$ versus sex and location. Because no differences were detected, one-way ANOVAs were used to compare $\delta^{13}C$ and $\delta^{15}N$ with location and time for all samples. Regression analysis was used to differentiate the time-series within tooth data as well as to compare large-scale trends for the total sample-set in temporal and spatial perspectives. An F-test for equal variances was used to determine consistency in variance of male versus female SSL, between geographic regions, and temporal changes before and after the regime shift. Significance was tested at the α = 0.05 level.

2.4 RESULTS

For all collagen samples, the overall % N and % C was 15.3 ± 0.94 % and 44.3 ± 2.94 % respectively, indicating that the samples tested were clean and representative of collagenous content in both the teeth and bone. The mean and variance of $\delta^{13}C$ and $\delta^{15}N$ values did not differ significantly between the two tissue types tested (bone: mean $\delta^{13}C$ = -13.8 ± 1.0 ‰, $\delta^{15}N$ = 17.3 ± 1.0 ‰; teeth: mean $\delta^{13}C$ = -13.8 ± 0.7 ‰, $\delta^{15}N$ = 17.8 ± 0.8

‰; $F_{[1,152]} = 1.0178$, $p = 0.457$). In order to compare data for teeth among SSL, it was necessary to establish if there was consistent enrichment or depletion in composition of teeth over time. The mean and variance of the 74 teeth did not differ systematically across all three segments (Table 2.1, Figure 2.3). There also were no differences between males (mean $\delta^{15}N = 17.5 \pm 0.9$ ‰, $\delta^{13}C = -13.8 \pm 1.0$ ‰) and females ($\delta^{15}N = 17.2 \pm 1.0$ ‰, $\delta^{13}C = -13.8 \pm 1.0$ ‰) over all locations for either $\delta^{15}N$ ($F_{[1,120]} = 1.063$, $p = 0.369$) or $\delta^{13}C$ ($F_{[1,120]} = 1.119$, $p = 0.27$). All samples were therefore used for comparisons of spatial and temporal patterns.

Using all samples, we observed slight variation in $\delta^{15}N$ and $\delta^{13}C$ composition with respect to location (Figure 2.4), with animals captured from western areas depleted in ^{15}N and ^{13}C (1.1 ‰ and 1.8 ‰, respectively) relative to those from eastern regions (nitrogen: $F_{[6,147]} = 7.24$, $p < 0.05$; carbon: $F_{[6,147]} = 10.5$, $p < 0.05$) over the whole study period. Focusing specifically on the period before the regime shift (1976), there was no difference between geographic locations in terms of $\delta^{15}N$ ($F_{[4,48]} = 0.77$, $p = 0.55$), but there was a significant difference observed in $\delta^{13}C$ ($F_{[4,48]} = 3.85$, $p < 0.05$).

Over the entire study period, mean $\delta^{15}N$ and $\delta^{13}C$ decreased by 0.5 ‰ and 1.0 ‰, respectively, with time (Figure 2.5; $\delta^{15}N = 18.6 - 0.013\text{Year}$, $R^2 = 0.02$, $p<0.05$, and $\delta^{13}C = -12.3 + 0.018\text{Year}$, $R^2 = 0.046$, $p<0.05$). There were small differences in pre- vs. post-regime shift (year 1976) mean stable isotopic values ($\delta^{15}N = 18.1 \pm 0.8$ ‰ vs. 17.6 ± 0.8 ‰ and $\delta^{13}C = -13.4 \pm 0.5$ ‰ vs. -14.0 ± 0.8 ‰, respectively). While the variance of $\delta^{15}N$ was not different between pre- and post- regime shift comparisons ($p = 0.479$), $\delta^{13}C$ had a significantly wider variance after 1976 than before ($p < 0.05$) (Figure 2.6). Overall, 48

out of 178 total post-1976 samples had a $\delta^{13}C \leq -14.4$ ‰. These trends were consistent along a geographic gradient and among regions where sample size was sufficient to test (with the exception of region 2 exhibiting no significant difference) (Table 2.2), as well as for tooth and bone sample types individually.

2.5 DISCUSSION

We observed no significant difference between bone and tooth samples of SSL. We were therefore able to directly compare both sources of collagen in further analyses. The tooth samples available for this study were restricted to adult females to attain dietary patterns of the population over the past 50 years. For the whole dataset, all 196 total animals were older than three years, thus eliminating the pre-weaning life history stage which has been shown to significantly alter the isotopic composition of teeth in early-year growth layers (Hobson and Sease 1998). Because of this control, the $\delta^{13}C$ and $\delta^{15}N$ values are representative of the species' temporal patterns versus physiological or behavioral changes in foraging. Examination of individual teeth (Figure 2.3), demonstrate no apparent systematic ontogenetic changes in either $\delta^{13}C$ or $\delta^{15}N$ over growth layers with time. The samples selected are therefore indeed from individuals beyond weaning and the data are representative of the population versus individual behavioral patterns. The slight, inconsistent, and non-significant trends in both isotopes with age throughout a tooth (Figure 2.3) aided the decision to utilize varying growth layers as true representations of temporal separation of animals and the population as a whole.

The surprising lack of differences observed in $\delta^{13}C$ and $\delta^{15}N$ range and mean values between the sexes confirmed the applicability of our fine-scale collagen sampling targeted on females. While the average trends of $\delta^{13}C$ and $\delta^{15}N$ composition were not different between the sexes, the highly migratory nature of males may still be misrepresenting the true regional trends of the species. Regardless, since no difference was observed between the sexes, all subsequent analyses of isotopic data reflect the combination of samples from both sexes.

The geographic patterns observed (Figure 2.4) are as expected but intriguing, as variations were observed in both isotopes throughout a longitudinal gradient. Variations in the $\delta^{13}C$ composition were as expected from such a broad geographic spread (Russia to California), and are indicative of oceanography and circulation patterns (Schell *et al.* 1998; deHart and Wooller 2004). Less predictable, though, are the patterns of ^{15}N depletion in more western regions. While the difference in $\delta^{15}N$ over the whole spatial range of approximately 1.0 ‰ does not represent a full trophic level, it is possible that the combination of $\delta^{15}N$ and $\delta^{13}C$ values observed from samples in more western regions is a result of those SSL feeding on lower trophic level fish species or more varied diets than those in the east. Much of this pattern could be driven, however, by the specific oceanographic influences (e.g., Oyashio and Kuroshio currents) on the primary productivity of the Kuril Islands (Dodimead *et al.* 1963; Shiomoto *et al.* 1994).

Due to low comparative sample size, a more detailed pre-and post-regime shift comparison was unfortunately not possible for the westernmost (Region 1) and an eastern (Region 6) regions (Table 2.2). The overall differences we observed throughout the whole

study region relative to specific geography, both before and after the regime shift, open up the possibility that there are small variations in the oceanographic forces acting on these vastly different areas (Sinclair *et al.* 2005). More specifically, the wide range of $\delta^{15}N$ and $\delta^{13}C$ values from animals in the central and western Aleutian islands (Regions 2 and 3; Figure 2.4) likely reflects the oceanographic and biological diversity of the region. This is consistent with the high productivity and range of isotopic values established for this Bering Sea "greenbelt" region (Springer *et al.* 1996; Schell *et al.* 1998).

Temporally, while the initial comparison yielded minor differences throughout the entire sample period, the variation of isotopic range in pre- vs. post-regime shift years presents an insight into fine-scale changes. When our data are plotted by yearly sampling average (± 1 SD) (Figure 2.5), it is apparent that there was an increase in the variance of $\delta^{13}C$ in SSL after the mid-1970's. This is also evident when data were included only from teeth, which have greater temporal specificity. The exception to this is found in samples from the coast of Russia, which likely reflect the variation in geographic source of carbon (Dodimead *et al.* 1963; Shiomoto *et al.* 1994) rather than difference in trophic level or prey type. Considering the interplay of the two isotopes, a large-scale feeding shift in fish species type or size could cause both $\delta^{15}N$ and $\delta^{13}C$ values to shift markedly at the start of the SSL decline. Given that we did not see this pattern, it is unlikely that the trophic level utilized by SSL have changed drastically over time. There was no significant change in $\delta^{15}N$ mean or variance either over a temporal gradient or corresponding with the regime shift. Therefore, the decreased survival of this species over the past 40 years seems unlikely to be due to a shift in foraging trophic level.

To confirm this, we must first determine how the $\delta^{15}N$ and $\delta^{13}C$ in SSL relate to their potential prey from their geographic range. Given the well-established isotopic fractionation between diet and the collagen of bone and teeth, there is an expected ~3 ‰ enrichment in ^{15}N and 1 ‰ enrichment in ^{13}C relative to prey (Kelly 2000; Kurle and Worthy 2002; deHart 2004). Given fractionation differences for ^{13}C between whole body (or muscle) and collagen, the total fractionation between diet and consumer collagen is 4-5 ‰. Using the total enrichment values of 4 ‰ and 4-5 ‰ for $\delta^{15}N$ and $\delta^{13}C$ respectively, we can estimate the differences in isotopic values of prey relative to temporal and spatial patterns. For SSL in westernmost regions, predicted mean prey $\delta^{15}N$ and $\delta^{13}C$ were likely 12.7 ‰ and -19.0 ‰, respectively.

These values correspond well with the typical values obtained for small, young pollock in the Bering Sea ($\delta^{15}N = 12.7 \pm 0.2$ ‰ and $\delta^{13}C = -18.3 \pm 0.1$ ‰ [-19.1 ± 0.1 ‰ for age 0 pollock]; Sinclair *et al.* 1994; Kurle and Worthy 2001). In contrast, for SSL in eastern-most regions, predicted average prey $\delta^{15}N$ and $\delta^{13}C$ for adult SSL were 13.8 ‰ and -17.2 ‰, respectively. These values are close to typical values for medium-sized Pacific herring ($\delta^{15}N = 13.5 \pm 0.1$ ‰ and $\delta^{13}C = -17.6 \pm 0.1$ ‰; Kurle and Worthy 2001), but are somewhat heavier than values for adult herring ($\delta^{15}N = 12.2 \pm 0.6$ ‰ and $\delta^{13}C = -20.7 \pm 0.7$ ‰; Hirons 2001). While it would be misleading to assume a single-source diet in these SSL, the results can provide a guide to dietary reconstruction.

Considering the observed change in variance of $\delta^{13}C$, these data alone could be taken to indicate either a shift in trophic level, feeding location (e.g., onshore vs. offshore), or changes in the $\delta^{13}C$ values of the base of the food chain (e.g., changes in

primary productivity). Schell (2000) suggested that the temporal change in $\delta^{13}C$ at a specific point in time (e.g., the regime shift) with no corresponding change in $\delta^{15}N$ (Figure 2.6) could be driven by altered primary productivity in the Bering Sea. This would be observed as a shift in the mean isotopic value, but not variance, which we do not detect. Rather, we observed a significant change in the variance of the $\delta^{13}C$ data which could indicate that SSL have shifted to consuming prey more rich in lipids, since lipids are often more depleted in ^{13}C relative to other biochemical components (Hobson *et al.* 1996; Roth and Hobson 2000; Kurle and Worthy 2002; deHart 2004). The more likely scenario, however, is that SSL were feeding in more offshore regions. This feeding in more offshore regions could have subsequently exposed SSL to greater risk from predation (Loughlin and York 2000). As described previously, the regime shift may represent a critical period about which major changes in primary productivity, and hence foraging behavior, occurred.

The coincidence in timing between the increase in the variability in $\delta^{13}C$ of SSL and the regime shift (1976) imply that there were higher trophic level consequences to this possible shift in primary productivity, and that these shifts may have caused SSL to search either in different areas (^{13}C-depleted, most pronounced in offshore regions), or for smaller or more varied species of fish after this event. Analyses of the $\delta^{13}C$ and $\delta^{15}N$ are insufficient to distinguish which of these hypotheses are most appropriate, however, and the results are compatible with either or both processes taking place. Comparing directly the prey values that are represented by the observed SSL isotopic composition, it suggests that the range of prey obtained pre-1976 ($\delta^{15}N$ = 12.0 to 16.5 ‰, and $\delta^{13}C$= -18.4 to -16.3

‰) could be composed of medium and large adult pollock, eulachon, medium-sized herring, and Pacific cod (Hirons 2001; Kurle and Worthy 2001). In contrast, the range of prey obtained after 1976 ($\delta^{15}N$ = 11.9 to 15.4 ‰, and $\delta^{13}C$= -20.1 to -16.6 ‰) most likely include, in addition to the eulachon and medium herring listed above, large quantities of young/smaller pollock and small herring (Kurle and Worthy 2001), which were not consumed prior to 1976. The isotopic values of large adult pollock lay outside the value range for post-1976 samples, and were therefore unlikely to compose any significant portion of the dietary input in these animals unless the isotopic values resulting from their consumption was counteracted by equal or greater consumption of prey at a much lower trophic level. Future work using advanced mixing models is suggested to elucidate these potential fine-scale diet combinations in SSL.

Given that there is, additionally, no geographic separation to this consistent $\delta^{13}C$ range extension and depletion, our results suggest that the regime shift event was a wide-spread and far-reaching event likely influencing the direct prey of the SSL. The ~1 ‰ decrease in the $\delta^{13}C$ of the atmosphere related to the burning of fossil fuels could decrease the $\delta^{13}C$ of photosynthetic organisms (e.g., phytoplankton) as has been suggested by Cullen *et al.* (2001). However, the apparent marked change in variance (Figure 2.5) that is coincident with the regime shift, does not seem to be consistent with a gradual change in the $\delta^{13}C$ value of the atmosphere since the start of the 20th Century. Similar to what was seen for bowhead whales (Lee 2000; Schell 2000; Schell 2001; Lee *et al.* 2005), the pattern in our data is not a direct effect of anthropogenic input, but rather must arise from a more abrupt change in productivity or foraging behavior.

This study has taken steps to address the major concerns and issues brought forth by previous isotopic studies on SSL. While a great deal is still to be learned given the lack of good prey data and further understanding of responses to environmental change, the comprehensive temporal and spatial dataset collection and incorporation of fine-scale temporal resolution in tooth sampling seems to demonstrate an influence of the regime shift on the foraging ecology of this species. The large-scale decline of the SSL was most likely caused by a myriad of factors. This study shows, though, that the regime shift in 1976, while possibly not a primary driver of this population collapse, may have affected SSL populations by limiting food-source acquisition, altering behavior, and modifying the food-web upwards from its base.

2.6 SUMMARY AND CONCLUSION

Our study has demonstrated the consistency and utility of analyzing tooth samples to indicate fine-scale patterns among SSL. The values obtained from the teeth were similar to and in concordance with those expected from prior processing of whole bone samples. The values obtained from each growth layer sectioned in the teeth of our study represent a range of years rather than a single time point. Finer sampling resolution in future studies could be performed to perfect the protocol, which could then yield increased temporal resolution. Tooth sampling in general can lead to reconstruction of population and ecosystem patterns otherwise prohibited by opportunistic bone sampling. The 46-year dataset, representing the years 1955-2001, and derived from samples taken across the entire range of the SSL, is the most comprehensive and representative to date. Given that

the shifts in isotopes observed could be driven by predation pressure on SSL or changes in productivity throughout their range in the nearshore regions, the results of this study reiterate that top-down ecosystem effects cannot be ruled out. Future studies exploring the issue of marine mammal population declines in this region should consider that there has indeed been a bottom-up trophic shift in the North Pacific over the past 40 years. There is likely a complex interplay of influences from all directions that have and will likely continue to affect pinniped populations.

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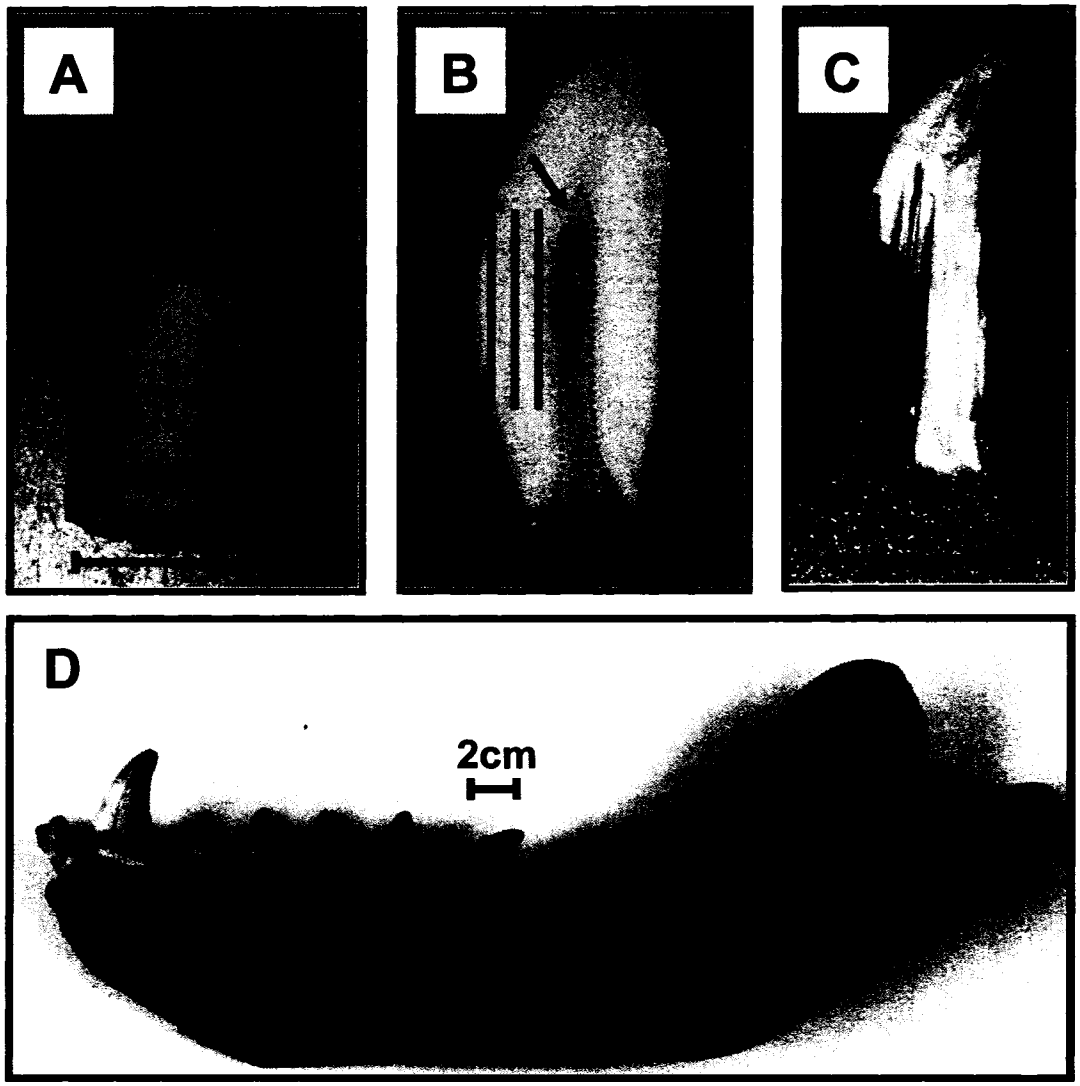

FIGURE 2.1. Diagrams of the sampling tissues and strategy of SSL tooth and mandible. Annuli are laid down from the pulp cavity (arrow on diagram B) distally. Teeth are displayed on the same scale, and are displayed as whole (A), longitudinally sectioned (B), and a thin subsection with the growth layers and samples removed (C). Sample selection site on the mandible (D) is denoted by a black triangle marking the approximate size and location. Image of sample #52246 was supplied by Jonathan Fiely and Link Olsen at the University of Alaska Museum.

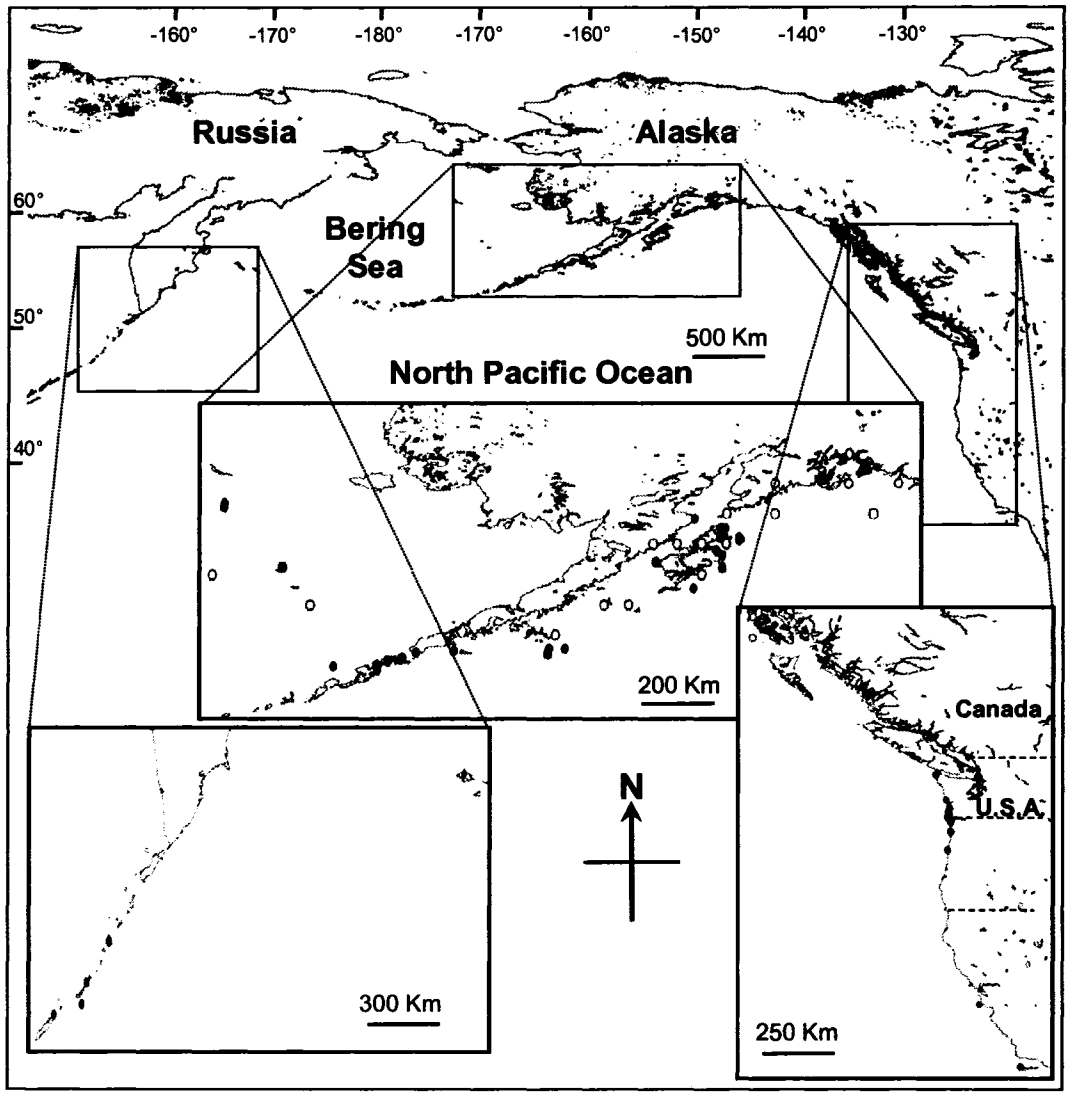

FIGURE 2.2. Locations of SSL from which bone (•) and teeth (○) were sampled. Sample locations represent the entire extent of the known SSL range (Loughlin et al., 1987).

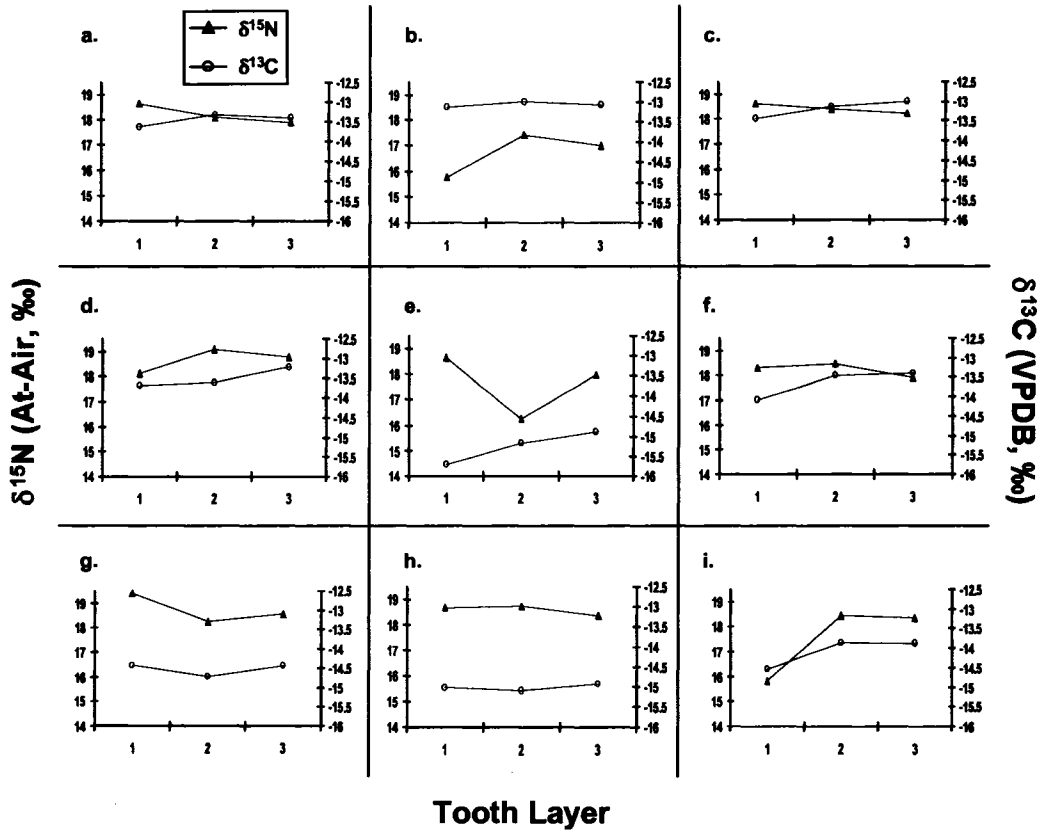

FIGURE 2.3. Sample ontogenetic changes of $\delta^{15}N$ (▲) and $\delta^{13}C$ (o) changes over the different sampled layers in nine representative teeth from before (a-c), during (d-f), and after (g-i) the regime shift. Tooth layers are labeled from 1 ("Outer" layer; material laid earliest in the animal's life) to 3 ("Inner" layer; material formed most recently, temporally nearest to the animal's death).

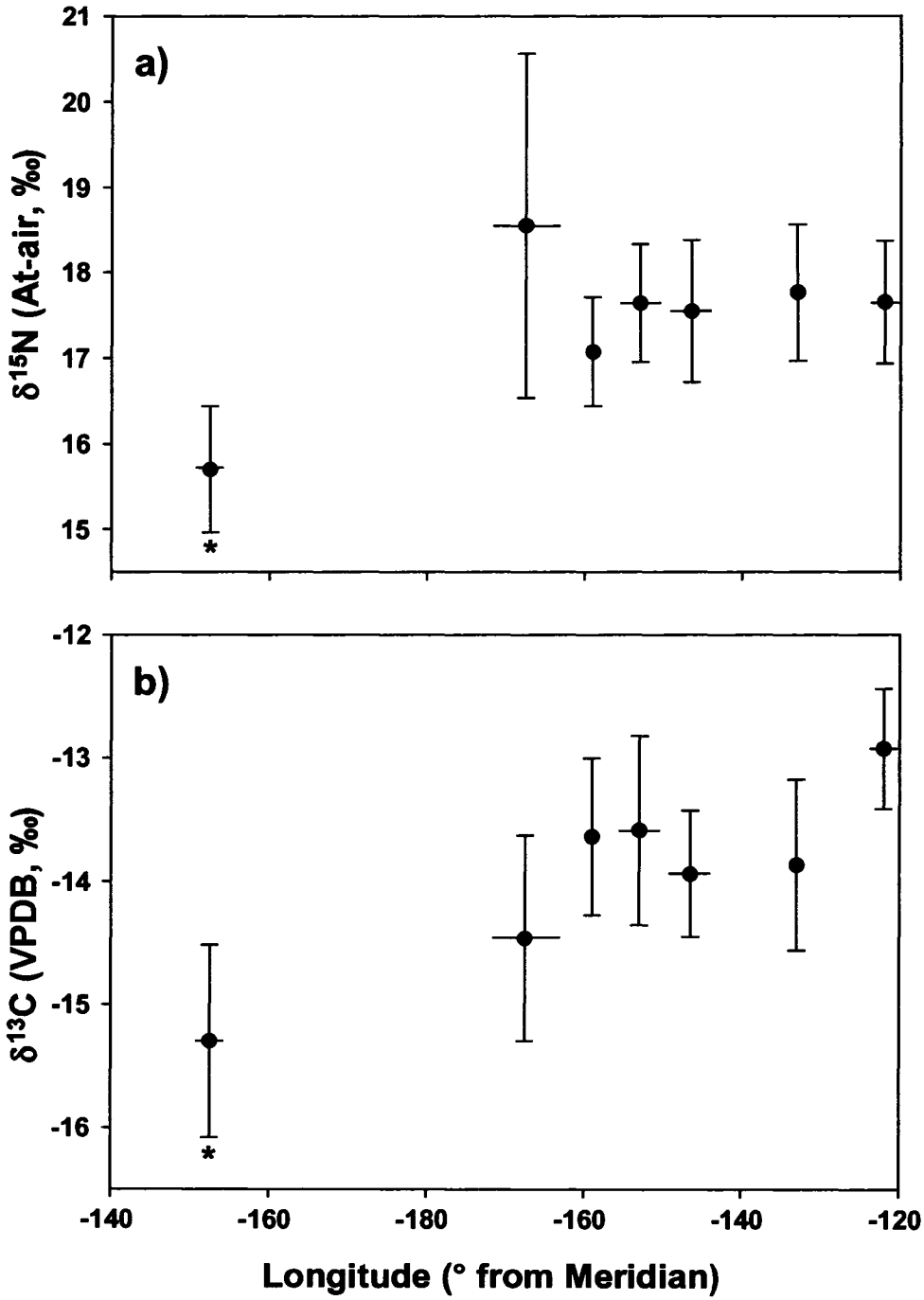

FIGURE 2.4. Average $\delta^{15}N$ (a) and $\delta^{13}C$ (b) measurements relative to sample site (expressed in degrees from Meridian). Vertical lines represent ± 1 standard deviation for averages; horizontal lines represent longitudinal spread of samples included. Values from samples taken from Russia are denoted with an asterisk (*).

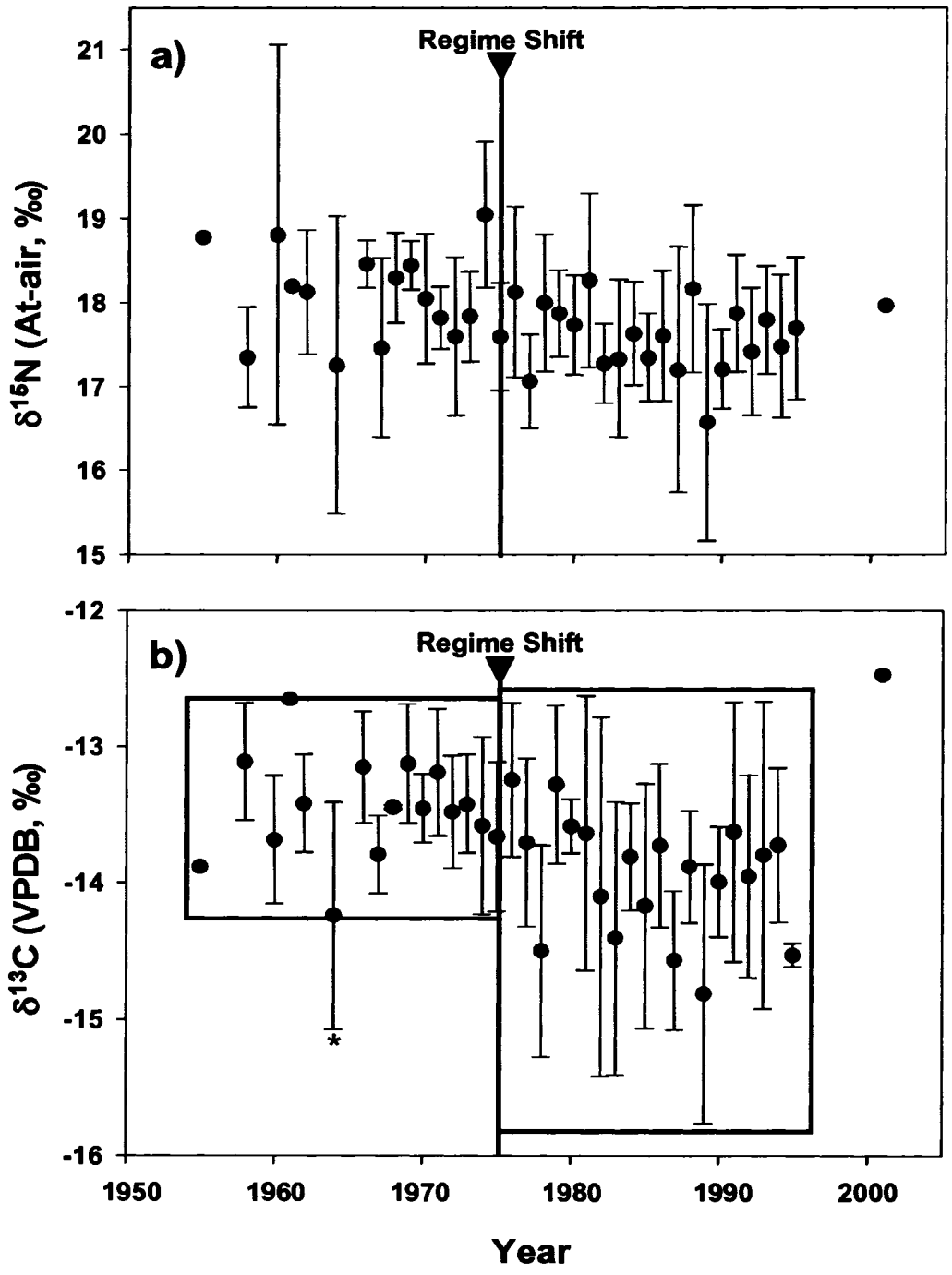

FIGURE 2.5. Average $\delta^{15}N$ (a) and $\delta^{13}C$ (b) measurements relative to sample year. Vertical lines represent ± 1 standard deviation for yearly averages. A vertical line represents a temporal separation in the range of values before and after 1976 (the regime shift). Values from samples taken solely from Russia are denoted by an asterisk (*).

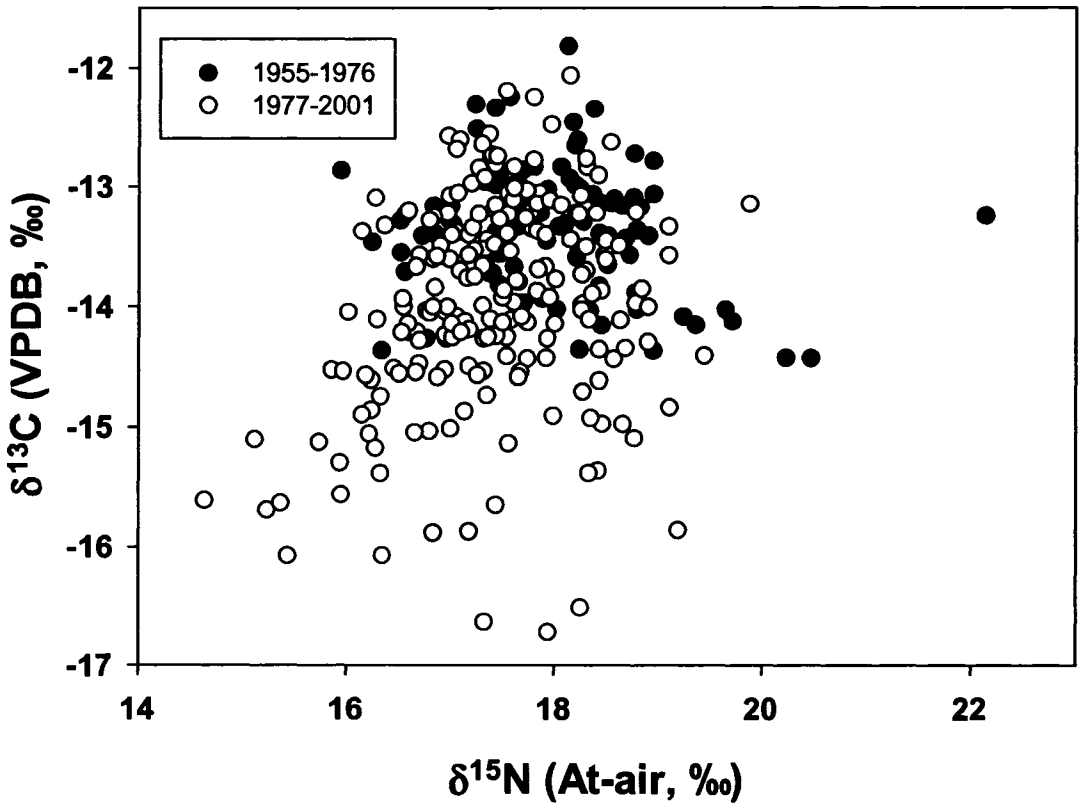

FIGURE 2.6. $\delta^{15}N$ and $\delta^{13}C$ values of all 316 total samples, separated with respect to years pre-regime shift (1955-1976 [•]), and post-regime shift (1977-2001 [○]).

Table 2.1. $\delta^{15}N$ and $\delta^{13}C$ values (± 1 SD, ‰) of the three different growth sections extracted from the 74 tooth samples. "Outer" sections represent material formed earliest in the animals' life, with "inner" representing the material formed most recently, closest in time to the animals' death.

Tooth Layer	$\delta^{15}N$	$\delta^{13}C$
Outer	18.1 (1.16)	-13.9 (0.78)
Middle	17.7 (0.84)	-13.7 (0.77)
Inner	17.5 (0.83)	-13.7 (0.73)

Table 2.2. Mean $\delta^{13}C$ and $\delta^{15}N$ values (‰) of Steller sea lions from the multiple regions throughout their range, both before and after the regime shift of 1976.

Region	Range (°)	Sample Type (*n*)		$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)		
		Teeth	Bone	Pre-1976	Post-1976	p-value	Pre-1976	Post-1976	p-value
1	-150E to -172E	-	14	-	-15.01	-	-	16.02	-
2	-173W to -168W	4	12	-14.50	-14.63	0.72	18.34	17.77	0.48
3	-167W to -158W	2	23	-13.47	-15.23	<0.05*	17.42	17.36	0.89
4	-157W to -149W	34	35	-13.19	-13.80	<0.05*	17.67	17.49	0.22
5	-148W to -144W	19	10	-13.35	-14.27	<0.05*	17.26	17.17	0.87
6	-134W to -132W	17	2	-	-13.86	-	-	17.79	-
7	-125W to -120W	-	24	-12.45	-12.89	<0.05*	17.8	17.56	0.43

CHAPTER 3

STABLE ISOTOPE ($\delta^{18}O$, δD) COMPOSITION OF THE WESTERN ARCTIC SEA-SCAPE: EXAMINING HABITATS OF THE BOWHEAD WHALE (*BALAENA MYSTICETUS*)[2]

3.1 ABSTRACT

Stable isotope analyses have been used in many different ecological applications to trace nutrient transfer, source location, and migratory behaviors of consumers. Much of this original research has focused on the use of the elements carbon, nitrogen, and sulphur. Given the more negative stable oxygen ($\delta^{18}O$) and hydrogen (δD) isotope compositions of freshwater sources (e.g., Mackenzie River = ~ -19 ‰, and ~ -150 ‰, respectively) versus the fairly constant $\delta^{18}O$ and δD values for ocean water (Standard Mean Ocean Water = ~ 0 ‰ for both $\delta^{18}O$ and δD) in the Arctic and sub-Arctic, we examined whether $\delta^{18}O$ and δD analyses could enhance our understanding of the western arctic bowhead whale (*Balaena mysticetus*) migratory behavior. To investigate these possibilities, we measured the $\delta^{18}O$ and δD in water and multiple zooplankton species along the migratory track (e.g., Bering Sea to Mackenzie Bay in the Beaufort Sea) of *B. mysticetus* to examine the isotopic variation in typical prey items. To complete the trophic perspective, baleen plates from six Alaskan *B. mysticetus* were sampled at 2 – 5 cm intervals and analyzed for their $\delta^{18}O$ and δD. Rather than a uniform stable isotopic

[2] deHart, P.A.P. and M.J. Wooller. Stable isotope ($\delta^{18}O$, δD) composition of the western Arctic sea-scape: examining habitats of the bowhead whale (*Balaena mysticetus*). Prepared for submission to Marine Ecology Progress Series.

composition, the $\delta^{18}O$ and δD values vary along the length of the baleen ($\delta^{18}O$ = 8 to 18 ‰; δD = -180 to -80 ‰). There was also a wide range in the values observed in the entire collection of zooplankton analyzed ($\delta^{18}O$ = -13 ‰ to 56 ‰; δD = -220 ‰ to -75 ‰). There was a clear regional separation in the zooplankton between the winter (Bering Sea) and summer (eastern Beaufort Sea region) habitat of the whales in terms of δD. Baleen samples not only confirmed the seasonal annual migration of the bowhead, but appeared to reflect the diet consumed in these two isotopically distinct regions. The results of this study suggest that oxygen and hydrogen isotope analyses could enhance ecological studies of marine systems at all trophic levels, including tracking shifts in long-term whale migration patterns due to environmental change.

Keywords: Bowhead whale, stable isotopes, migration, baleen, western Arctic, Bering Sea, Beaufort Sea

3.2 INTRODUCTION

The bowhead whale (*Balaena mysticetus*) is a large baleen whale residing in circumpolar waters in the northern hemisphere. The largest management stock of this species is found in the areas of the Western Arctic, extending from the Bering to the Chukchi and Beaufort seas (George et al. 2004). The latest population estimate for this particular stock is nearly 10,500 individuals, increasing at a rate of approximately 3.4 % per year (George et al. 2004). The whales in this stock broadly follow a typical yearly migratory pattern (Fig. 3.1), between the Bering Sea in the winter, through the Bering Strait

and the northern Chukchi Sea, to the eastern Beaufort Sea and Mackenzie Bay for the warmer, more ice-free months (Moore and Reeves 1993). The return trip prompted by the expansion in extent of sea ice during the fall and winter takes the whales back along the coast of northern Alaska and perhaps the northeastern coast of Russia on their way back to the Bering Sea (Schell et al. 1988, Moore and Reeves 1993).

Bowhead whales feed on an array of zooplankton in the water column, with the majority of species divided between copepods and euphausiids (Schell et al. 1989, Schell 1992, Lowry 1993, Lee et al. 2005). The feeding habits of bowheads throughout their migration are well established and recent studies provide insight into the relative amounts of food consumed from various parts of the seasonal range (Hoekstra et al. 2002, Lee et al. 2005). Additionally, research that examined the various levels of productivity throughout the extent of the migratory range of the bowhead concluded that feeding in the eastern Beaufort Sea and Mackenzie River outflow region are important to the survival of this species (Schell 2000, 2001).

Animals that regularly move across isotopic gradients during seasonal migrations can acquire distinct isotopic signatures along their migratory path and record them in their tissues (e.g., Deniro and Epstein 1978, Peterson and Fry 1987, Hobson and Welch 1992, Greenberg et al. 1997, Burton and Koch 1999, Hobson 1999, Webster et al. 2002). Soft tissues, such as blood and fat, are constantly regenerating and this turnover continuously alters their stable isotopic composition. However, some tissues are laid down incrementally (e.g., teeth, hair, nails, and feathers) and provide an isotopic record of an animal's migratory and feeding history (Peterson and Fry 1987, Schell et al. 1988, Koch et al. 1989, Schell et al.

1989, Hobson and Welch 1992, Michener and Schell 1994, Hobson 1999). In bowhead whales, keratinous tissue is laid down incrementally in the form of baleen plates. The stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope composition of keratin along these plates have been analyzed previously and provided insight into both habitat usage and relative quantities of food derived from various areas (Schell et al. 1988, 1999, Dunton et al. 1989, Lowry 1993, Michener and Schell 1994, Lee et al. 2005). The $\delta^{13}C$ and $\delta^{15}N$ isotope data for these whales (Schell et al. 1984, Schell 1992, 1998, Lee et al. 2005) also provide an excellent baseline of the relative isotopic variability among organisms in this region. However, they are insufficient to definitively identify the source location of the prey items sustaining bowhead whales (Schell 1998). In some instances analyses of the stable oxygen and hydrogen isotopic composition ($\delta^{18}O$ and δD) of inorganic and organic animal tissues have been performed and can assist in comprehending animal migration patterns (Estep and Dabrowski 1980, Koch et al. 1989, Hobson 1999, Hobson et al. 1999, Bowen et al. 2005). While the majority of these studies have focused on terrestrial animals, some illustrate that migratory behavior can be discerned for animals migrating between marine habitats (Knoche et al. 2006, Greenberg et al. 2006, Whitledge et al. in press).

While mean ocean water has $\delta^{18}O$ and δD values varying only slightly from 0 ‰ (± 1 ‰) unless in restrictive basins or near freshwater inputs, continental water varies over a wide range (Gat 1996, Kendall and Coplen 2001, Bowen and Wilkinson 2002, Bowen 2005). This difference between continental and marine systems is most marked in higher latitudes, providing great potential for enhancing our understanding of migratory behavior for animals that pass between continental and marine dominated waters (Bowen et al.

2005). In general, the $\delta^{18}O$ of fresh continental water ranges from 3 ‰ to less than -50 ‰ and from 0 ‰ to -270 ‰ for δD, with the most negative values being evident in the Arctic and sub-Arctic (Bowen and Wilkinson 2002, Bowen et al. 2005). A visual display of this range, the Global Meteoric Water Line (GMWL), is essentially the baseline for variation in $\delta^{18}O$ and δD worldwide, as it is an average of local or regional meteoric water lines which vary in both slope and intercept according to meteorological conditions (Craig 1961).

Although bowhead whales do not migrate between continental and marine ecosystems, they do pass between areas of the ocean composed more heavily by continental-derived precipitation (e.g., outflow from major river systems). For instance, the summer feeding areas of bowheads are subject to large inputs of continental water from the Mackenzie River (Macdonald et al. 1987). In particular reference to the western arctic stock of the bowhead whale, the surface water in the Mackenzie River drainage basin has much lower $\delta^{18}O$ and δD (-18‰ and -150‰, respectively) relative to SMOW (Schmidt et al. 1999).

Given this large variation in $\delta^{18}O$ and δD between the two migratory endpoints for bowheads, the Mackenzie delta and the Bering Sea, we hypothesize that these isotopic variations should be reflected in the biota that inhabit (e.g., zooplankton) or migrate between (e.g., bowheads) these two regions. We examined the baleen from six whales sampled from 1955-1986, to test the hypothesis that seasonal migrations would be depicted in terms of $\delta^{18}O$ and δD variation in baleen. We expected to see samples from whales in the summer months to be more depleted than those from whales in the Bering

Sea during the winter. More specifically, we hypothesized that the portions of bowhead whale baleen plate laid down during the time the whales are thought to have been off of the Mackenzie Delta (as defined by Schell 1998, 2000, Lee et al. 2005) should have more negative $\delta^{18}O$ and δD values compared with those portions laid down while the animals resided in the Bering Sea. We also hypothesized that, since bowheads do not actually ingest sea water (Schell et al. 1989, Lowry 1993, Lee et al. 2005), any $\delta^{18}O$ and δD variation in the baleen plate is a result of isotopic variation in their prey. We therefore proposed that prey in the different regions along the migratory route should be different. Prey from the Beaufort Sea/Mackenzie Delta region should have $\delta^{18}O$ and δD values more negative than from the open ocean/Bering Sea region. We propose that if the $\delta^{18}O$ and δD of the bowhead prey, zooplankton, are the major drivers of the isotopic composition of baleen keratin, then keratin should more closely resemble their prey rather than the ocean water through which they pass.

Recent studies propose that, while δD of keratin in higher order terrestrial mammals is biochemically and isotopically derived partially from drinking water, species with marine-based dietary components or with access to food from isotopically diverse sources may be at least partially decoupled from the influence of local water (Hobson et al. 1999, Sharp et al. 2003). A competing hypothesis is that the whales display values similar to that of the water they seasonally inhabit with consistent and predictable fractionation, but are not trophically enriched relative to their prey. If this were the case, it would seem that these whales are not obtaining their body water solely from their prey (Lowry 1993), but, contrary to current understanding of their life history, WABW may be

somehow partially ingesting water directly from their environment. In addressing these hypotheses, our primary goal was to assess the viability of using $\delta^{18}O$ and δD analyses of keratin laid down in baleen plates to trace bowhead whale seasonal migration patterns.

3.3 MATERIALS AND METHODS

We analyzed samples archived at the Alaska stable Isotope Facility (ASIF) from six baleen plates compiled by D. Schell and collected via a joint effort of NOAA-NMFS, Alaska Native Subsistence Hunters, and the Alaska Department of Fish and Game (Table 3.1). Supporting data were available prior to the analysis of these samples, including age, size, sex, condition, and location of death (Schell 2000). Samples were taken at 2-5 cm intervals along the whole length of the baleen. These keratinous tissue samples provide a temporal record of whale migration over the animal's life and represent a 31-year period from 1955 to 1986.

Zooplankton samples from the waters of the northern Chukchi Sea eastward to the Admunsen Gulf were sub-sampled from a research cruise collection in 2002 to the Canada Basin (Fig. 3.1) and contained species from the surface, mid-water column, and benthic sampling. A detailed description of the investigation area and oceanographic features of this cruise were presented by Iken et al. (2005). A total of 55 samples were analyzed, of which 26 were crustaceans and 7 were calanoid copepods (*Calanus hyperboreus*). These samples were taxonomically segregated for data comparison and statistical analysis. Surface water ($n = 24$) and zooplankton ($n = 32$) samples (*C. hyperboreus*) from the Bering Sea were obtained during a Bering-Aleutian Salmon International Survey (BASIS) cruise from September 5 to October 8, 2002 (Fig. 3.1). Surface water samples were filtered to remove phytoplankton then

frozen aboard ship for transport back to the laboratory. Water isotope ($\delta^{18}O$ and δD) values from the Canada Basin region were obtained from the NASA GISS-Global Seawater Database (Schmidt et al. 1999) and categorized into one of two geographic regions, Bering Sea or Beaufort Sea, for analyses. Zooplankton species subsampled from the larger sampling effort are specific to copepods, and spread geographically over all oceanographic regimes of the region. For both regions, organisms were picked from a plankton sample and deposited into small vials. They were frozen without water on the ship, subsequently freeze-dried in the laboratory before being ground and weighed into tin capsules for stable isotope analyses (see below).

For solid organic samples (e.g., keratin), the finely powdered, dried, and homogenous zooplankton and baleen were weighed into tin capsules (3 x 3 mm; approximately 0.3 mg powder) that were each subsequently crimped shut. These samples were loaded into an autosampler (Costech Zero-Blank autosampler) and analyzed using a Thermo Finnigan Delta^{plus}XL stable isotope ratio mass spectrometer (IRMS). This instrument was interfaced with a Thermoquest high temperature conversion elemental analyzer (TC/EA). Each sample was pyrolyzed into H_2 and CO gases then separated chromatographically. These gases were then conveyed through a Finnigan Conflo III system to the IRMS with a continuous flow of Helium carrier gas.

The measurements obtained are expressed in standard delta (δ) notation, as parts per thousand (‰). Ratios were expressed as:

$\delta^{18}O$ or $\delta D = [(R_{sample}/R_{standard})-1] \times 1{,}000$

where R_{sample} and $R_{standard}$ are the ratios of $^{18}O/^{16}O$ or $^{2}H/H$ for the sample and standard, respectively.

δD and $\delta^{18}O$ values are reported relative to Vienna-Standard Mean Ocean Water (V-SMOW). For quality control, empty tin capsules were analyzed every twenty samples and working standards (benzoic acid [Fisher scientific, Lot No. 947459]) were analyzed every ten samples. The entire run was calibrated relative to BWBII, as well as the National Institute of Standards and Technology (NIST) standards NBS-19, NBS-22, NBS-30, PEF-1, and sucrose ANU, which formed a calibration curve with an r^2 of >0.99. Analytical precision based on the standard deviation of benzoic acid reference checks for $\delta^{18}O$ and δD ranged from 0.2 to 2.2 for oxygen and 1.0 to 8.4 for hydrogen. The % oxygen precision ranged from 0.4 to 0.8, while % hydrogen precision ranged from 0.1 to 1.3.

For water samples, 0.2 uL of water sample were injected into the TC/EA with a CTC Analytics A200SE liquid autosampler. Each sample was pyrolyzed into H_2 and CO gases then separated chromatigraphically. These gases were then transferred through a Conflo III system to the IRMS where the stable isotopic compositions of the gases were analyzed. The δD and $\delta^{18}O$ of water samples are also expressed in standard ‰ relative to V-SMOW. The δD and $\delta^{18}O$ of water samples were calibrated relative to the international isotope standards V-SMOW, GISP, and SLAP, which gave a calibration curve with an r^2 of >0.99. All water samples were run in triplicate, and laboratory working standards were analyzed every seventh replicate sample. Data are expressed throughout as mean ± 1 standard deviation (SD).

For similar studies analyzing δD of organic substances (e.g., keratin), issues related to hydrogen exchange have been described by others (e.g., Wassenaar and Hobson 2002). We therefore adopted a protocol consistent with that outlined by Wassenaar and Hobson (2002) where samples and a calibrated keratin standard (BWBII; calibrated δD = -108.2 ‰; Hobson *et al.* 1999) were "air-equilibrated" with ambient laboratory air moisture in ASIF at room temperature for more than 96 hours prior to δD analysis. After more than 96 hours of equilibration, all samples and standards were loaded into the autosampler of the TC/EA-IRMS. The δD of sample hydrogen was calculated by measurement of HD isotopes (after standard H^{3+} corrections) and comparison to a pulse of monitoring H_2 gas (research grade 99.99 %; V-SMOW). Analysis of BWBII yielded a δD of -109.1 ‰. The ‰ difference (0.9 ‰) between this value for BWBII and its calibrated value (-108.2 ‰; Hobson et al. 1999) is consistent with the lower range of our δD analytical precision (1.0 ‰).

3.4 RESULTS

3.41 Stable isotope composition of water

The δD and $\delta^{18}O$ of water values obtained from the seawater database fell along the Global Meteoric Water Line (GMWL) (Fig. 3.2) with a $y = 8x + 10$ relationship between δD and $\delta^{18}O$. There was a direct overlap in range and amplitude of the values from both the Bering and Beaufort sea regions (Fig. 3.2). However, the most depleted δD and $\delta^{18}O$ values were in the sample set from the Beaufort Sea. The mean values from the Bering Sea and Beaufort Sea were not significantly different (Table 3.2), but the

variance in both isotopes was much greater in samples from the Beaufort Sea (F-test for variance, $p < 0.05$) (Fig. 3.2).

3.42 Stable isotope composition of zooplankton

A regression analysis of the water analyzed from the Bering Sea with the corresponding zooplankton samples from the same locations yielded a stronger positive relationship for δD ($R^2 = 0.1326$; $y = 2.225x - 129.34$) than for $\delta^{18}O$ ($R^2 = 0.0083$; $y = 0.6521x + 18.357$); (Fig. 3.3), but neither comparison was significant or suggested a strong relationship. Over all the zooplankton samples analyzed, there was a wide range in the stable isotopic values ($\delta^{18}O$ = -13 ‰ to 56 ‰; δD = -220 ‰ to -75 ‰); (Fig. 3.4), and a clear regional separation in the zooplankton between the winter (Bering Sea) and summer (eastern Beaufort Sea) habitat of the whales. No statistical difference was observed between the two regions with respect to % concentration of oxygen (Beaufort Mean = 22.2 ± 3.2; Bering Mean = 23.6 ± 4.8; $p = 0.109$) or % concentration of hydrogen (Beaufort Mean = 6.4 ± 2.2; Bering Mean = 7.0 ± 2.1; $p = 0.175$). While the mean δD and $\delta^{18}O$ values for the copepods collected in the Bering Sea (δD = -149.2 ± 16.2 ‰ and $\delta^{18}O$ = 17.1 ± 3.3 ‰) did not differ statistically from the entire sample set from the Beaufort region ($p=0.412$), significant differences were observed for crustaceans (δD = -166.3 ± 29.4 ‰, $p < 0.05$, and $\delta^{18}O$ = 25.8 ± 9.5 ‰, $p < 0.05$). Most appropriate, however, is a direct species comparison between copepods (*C. hyperboreus*) from the Beaufort region (δD = -191.5 ± 5.9 ‰ and $\delta^{18}O$ = 21.8 ± 5.5 ‰) with those from the Bering region, which displayed isotopically distinct and statistically significant

differences in δD, but not $\delta^{18}O$ (Table 3.2). *C. hyperboreus* samples were isotopically indistinguishable relative to fine-scale specific regions (e.g., central Bering vs. Bering Strait and Mackenzie Bay vs. central Beaufort) from which they were sampled. Zooplankton were isotopically enriched relative to the δD and $\delta^{18}O$ of the water from the region.

3.43 Stable isotope composition of bowhead baleen plates

Rather than uniform stable isotopic compositions, both the $\delta^{18}O$ and δD values varied greatly along the length of the baleen ($\delta^{18}O$ = 8 to 18 ‰; δD = -155 to -80 ‰). The variation along the baleen appeared to correspond to the annual migration of bowheads previously illustrated by Schell et al. (1988) using stable carbon and nitrogen isotopes (Fig. 3.5). Compiling the average isotopic signatures per year for all of the whales analyzed, the $\delta^{18}O$ and δD display very different patterns (Fig. 3.6). Throughout the period of examination, there is a net change of ~10 ‰ in average $\delta^{18}O$ from 1955 to 1986 and an increase throughout the years. This change is observed in both the summer and winter month peak averages. While there is an observed cyclical seasonal signature in both $\delta^{18}O$ and δD for all whales (Fig. 3.6), δD signatures appear to follow the cycles of $\delta^{13}C$ and $\delta^{15}N$ more consistently than $\delta^{18}O$. There was a clear and significant difference between the average isotopic values for all whales between the summer and winter months for hydrogen, and to a lesser extent oxygen (Table 3.2). These seasonal differences correspond with those observed between copepod $\delta^{18}O$ and δD between the two regions (Fig. 3.7).

3.5 DISCUSSION

3.51 The $\delta^{18}O$ and δD of the bowhead whale environment

The $\delta^{18}O$ and δD of water were similar between the Bering and Beaufort Sea regions (Fig. 3.2). The lower $\delta^{18}O$ and δD expected for the Beaufort Sea region may have been overshadowed by the incorporation of values from more offshore regions of the eastern and western Beaufort Sea. These sample selection points were chosen from the global seawater database to match cruise sample locations of the zooplankton and are likely an accurate representation of the water source utilized by the prey of bowhead whales (Fig. 3.3). This overlap between the Beaufort and Bering seas underscores the validity of the expected isotopic difference between freshwater and mean ocean water (Schmidt et al. 1999, Bowen and Wilkinson 2002, Bowen et al. 2005). Future sampling should include direct paired water and prey samples to obtain the most precise representation of the regions.

3.52 The $\delta^{18}O$ and δD of bowhead prey

There is a weak positive relationship between the $\delta^{18}O$ and δD of water from the Bering Sea and the $\delta^{18}O$ and δD of zooplankton from the same region (Figs. 3.3a, 3.3b). Both figures highlight that while ocean water is relatively consistent isotopically in a single region, $\delta^{18}O$ and δD from a single species have a wide variation in values (~10 ‰ in $\delta^{18}O$ and ~60 ‰ in δD).

While prior publications (Schell et al. 1984, 1988, 1989, 1998) suggest that carbon isotope fluctuations likely result from the uptake of ^{13}C-depleted material injected into the Mackenzie Delta by upwelling of nearby deep Arctic Ocean waters, this is probably not the case in the current study. The said effect would not likely influence the oxygen or hydrogen isotope content given the uniformity of ocean water δD and $\delta^{18}O$. Upwelling water should be relatively consistent with shallow water in terms of δD and $\delta^{18}O$ in this region (MacDonald et al. 1987, Grebmeier and Barry 1991, McLaughlin et al. 2005).

We hypothesized that the δD and $\delta^{18}O$ of zooplankton should be higher relative to the water in which they were found. This would be consistent with other studies on plants and animals relative to the waters in which they live (Schimmelmann and Deniro 1986, Sauer et al. 2001, Wooller et al. 2004, Whitledge et al. In press). For instance, it has been established that the $\delta^{18}O$ of cellulose in a plant is predictably approximately 27 ‰ higher relative to the water in its environment (Epstein and Mayeda 1953, Epstein and Yapp 1976, Sternberg et al. 1986a, 1986b, Sauer et al. 2001, McCarroll and Loader 2004). This fractionation takes place as a result of carbohydrate and cellulose synthesis (Sauer et al. 2001, McCarroll and Loader 2004).

Chitin from marine arthropods has also been found to be enriched in ^{18}O by approximately 26 ‰ relative to mean ocean water (Schimmelmann and Deniro 1986). Head-capsules composed primarily of chitin from freshwater invertebrates (Chironomids) have also been found to consistently be ~27 ‰ higher than the lake water in which they lived (Wooller et al. 2004). While there have been some similar estimates of fractionation for highly migratory species (e.g., ~30 ‰ for neotropical migrant songbirds) in terrestrial

and freshwater environments (Hobson and Wassenaar 1997), there are currently no such estimates for δD in the literature base for a similar marine environment (see Sharp et al. 2003). In this study, we do not observe a 26-27 ‰ fractionation in $\delta^{18}O$ of the zooplankton relative to the water in which they lived. Rather the fractionation between the water and plankton tested ranged from 14 to 25 ‰ (mean = 18 ‰) for $\delta^{18}O$ and -155 to -105 ‰ (mean = -142 ‰) for δD (Fig. 3.3). The magnitude of this difference could be a result of having unpaired water and zooplankton sample locations. It is also likely that incorporation of the phytoplankton for these regions could yield further insight into this fractionation. Some of the variation in the prey may also be the result of differences in the proportions of various compositional compounds (e.g., lipids versus sugars). Different compounds may each also be associated with different fractionations during their synthesis. Future work on the diet items of WABW could focus on compound specific analyses to decipher the role these variations serve in the isotopic values of this region.

A comparison of the zooplankton samples between the two regions (Bering vs. Beaufort Seas) reveals more apparent differences. The wide range in the values observed for all samples in the initial analysis is expected, given the large variety of taxa (34 different species) included from sampling in the Beaufort Sea region (Fig. 3.4). Species-specific separation focusing on the primary prey of bowheads from both regions, calanoid copepods (Lee et al. 2005), showed a clear regional separation in the zooplankton between the winter and summer habitat of the whales in terms of δD (Fig. 3.4). The $\delta^{18}O$ do not follow the same pattern, showing virtually no difference between the two regions. This may be due to the small overall degree of variation in $\delta^{18}O$ in the environment

compared with δD (Table 3.2). An alternative explanation for this trend is that hydrogen is selectively taken up by zooplankton utilizing another physiological mechanism that requires limited internal processing and thus less variation between the tissue of the prey and the water source, as has been illustrated for humans (Frazer et al. 1997). Given the wide geographic range of prey samples (Fig. 3.1), it is also possible that there are regional differences in the zooplankton component within the Beaufort sampling region. There may also be differences due to a temperature dependent fractionation, influencing the phytoplankton trophic level, as has been shown for various terrestrial plants (Sternberg et al. 1986b).

3.53 The bowhead whale

Scaling this study out to the samples of whale baleen, the data plot in Fig. 3.5 is typical of the results in this study, displaying (in this case: four) distinct minima throughout the length of the baleen in all four stable isotopes ($\delta^{13}C$, $\delta^{15}N$, δD, and $\delta^{18}O$). The repetition of minima observed in the $\delta^{18}O$ and δD data tracks similar patterns to those exhibited by the $\delta^{13}C$ and $\delta^{15}N$ data shown by Schell et al. (1988, 1999). In a previously published report using samples from this same whale, Schell et al. (1988) found that the minima in the $\delta^{13}C$ and $\delta^{15}N$ are attributed to baleen produced from isotopically-depleted nutrients consumed during summer feeding in the vicinity of the mouth of the Mackenzie River (Schell et al. 1988). Each minimum value shown for the elements represents summer in a different year in all four plots, so that, from left to right, the minima are from 1974, 1975, 1976, and 1977. Throughout the life of this particular

whale, the amplitude and range of values in $\delta^{18}O$ and δD increase with age for the entire baleen, and may be due to environmental factors affecting the entire population in the late 1970s rather than behavioral patterns (deHart et al. 2005, deHart et al. 2006).

It is promising to see that $\delta^{18}O$ and δD reflect the migratory history of the bowhead whale. These fine-scale changes in the isotopes over time may indeed yield more detailed information on the exact migratory route, seasonal behavior, and/or environmental variables affecting all whales in this region. When considering the combined results of all the whales in this study (Fig. 3.6), $\delta^{18}O$ and δD fluctuations with time are less clear. The mean $\delta^{18}O$ varies from 12.3 ‰ (1964) to 18.9 ‰ (1986) for winter and 10.7 ‰ (1955) to 19.0 ‰ (1986) for summer (Fig. 3.6b). The mean δD varies from -108.9 ‰ (1956) to -89.7 ‰ (1965) for winter and -141.4 ‰ (1960) to -114.5 ‰ (1961) for summer (Fig. 3.6a). Even though some increases in $\delta^{18}O$ and δD over time may be due to growth (e.g., ontogenetic effects) and shifts in diet and migratory behavior, the fact that this pattern is observed in all the whales (of different ages and sexes) over time suggests that the changes are driven by environmental influences.

Schell et al. (1988) attributed similar fluctuations in $\delta^{13}C$ baseline values in baleen from other bowhead whales to annual shifts in the ^{13}C content of plankton consumed in the Bering and Chukchi seas. It has been argued that these variations in $\delta^{13}C$ may be due to alterations in the whales' migration and feeding patterns and changes in ocean productivity (Schell 1998, 2000). The $\delta^{18}O$ and δD variations in this study are more likely the result of migration and feeding pattern changes rather than being caused by variations in ocean productivity.

The entire collection of $\delta^{18}O$ and δD values recorded for baleen are significantly higher relative to standard mean ocean water ($\delta^{18}O_{V\text{-}SMOW}$ and $\delta D_{V\text{-}SMOW}$ = 0 ‰). This could have resulted from various biochemical fractionations associated with assimilation of prey and synthesis of keratin. The primary crustaceans in the diet of baleen whales have, in turn, fed on phytoplankton (Schell and Saupe 1998). It is assumed that, given the nature of bonding between hydrogen and oxygen, that both of these elements undergo similar processing and fractionation in higher order animals (Estep and Dabrowski 1980, Kohn 1996, Bowen et al. 2005). The $\delta^{18}O$ and δD of diet items (prey) should be passed on to whales, with an additional fractionation possibly associated with trophic level. Minima in the average $\delta^{18}O$ and δD of all whales probably represent the influence of consumption of isotopically depleted material discharged into the Beaufort Sea by the Mackenzie River, while maxima are likely the result of assimilating material from the Bering Sea (Fig. 3.7). This material may be baleen precursors (amino acids from zooplankton) depleted in $\delta^{18}O$ and δD from formation in an environment with a high proportion of fresh river water influence. More likely, however, the oxygen and hydrogen consumed by and subsequently enriched in the whale is rooted in ocean water, diluted by continental water and incorporated into the whale as the body water from prey. This body water is then likely equilibrated with structural oxygen and hydrogen during baleen synthesis, similar to what occurs in the synthesis of other animal tissues (Schimmelmann and Deniro 1986, Kohn 1996, Visser et al. 2000, Smith et al. 2002, Nelson 2005).

The disparity in patterns observed between $\delta^{18}O$ and δD is intriguing but perplexing. While the seasonal variation in δD of baleen for all WABW follows a clear seasonal pattern (Fig. 3.6a), the cyclical nature observed in individual baleen for both $\delta^{18}O$ and δD (Fig. 3.5) is not observed when values are averaged for $\delta^{18}O$ (Fig. 3.6b). In addition, there appear to be increasing mean and variance in $\delta^{18}O$ for whales in more recent years. This difference between $\delta^{18}O$ and δD could mean that either the two isotopes are indicators of different environmental patterns, or they are processed in a different manner through the physiology of the organism. While there has been research into the relationship of animal δD to prey and environmental water components (Estep and Dabrowski 1980, Hobson and Wassenaar 1997, Hobson et al. 1999, Wassenaar and Hobson 2002, Sharp et al. 2003, Whitledge et al. In press), little conclusive evidence accounting for the trends in $\delta^{18}O$ has been presented (Bowen et al. 2005). While the δD signature may be a direct refection of changes in WABW migration forced by sea ice patterns (deHart et al. In prep), the increase in $\delta^{18}O$ with time (Fig. 3.6b) may rather be following trends of increased temperature (IPCC 2001, Karl and Trenberth 2003, ACIA 2004). Some studies on terrestrial plants indicate that there may indeed be a difference between mechanisms (e.g., changes in temperature versus water uptake) driving the different patterns of δD versus $\delta^{18}O$ (Sternberg et al. 1986b, McCarroll and Loader 2004). This potentially temperature-driven $\delta^{18}O$ pattern in WABW baleen may be driven at the phytoplankton level, which has yet to be tested. On the other hand, the trend in $\delta^{18}O$ signature we see is unlikely being driven by long-term environmental changes in the

^{18}O composition of CO_2 or O_2. The ^{18}O in both CO_2 and O_2 has remained relatively constant (0.5 ‰, http://instaar.colorado.edu/sil/research), especially in relation to the variation we see in the $\delta^{18}O$ of WABW baleen (~10 ‰) over the study period. Therefore, further examinations focusing on more recent WABW baleen overlapping with current climate warming, as well as testing of the δD and $\delta^{18}O$ of regional phytoplankton, should help to clarify how closely $\delta^{18}O$ in whales follow the changing temperature record.

3.6 SUMMARY AND CONCLUSIONS

As was originally the case with $\delta^{13}C$ and $\delta^{15}N$ of baleen plates, $\delta^{18}O$ and δD analyses provide a novel perspective of the annual migration of bowhead whales. The $\delta^{18}O$ and δD values vary along the length of the baleen ($\delta^{18}O$ = 8 to 18 ‰; δD = -180 to -80 ‰), and we observed a wide range in the values observed in the zooplankton ($\delta^{18}O$ = -13 ‰ to 56 ‰; δD = -220 ‰ to -75 ‰). Species-specific zooplankton separation showed closely paired patterns with regional water values, and there was a clear regional separation in the zooplankton between the winter (Bering Sea) and summer (eastern Beaufort Sea region) habitat of the whales in terms of δD. Baleen samples not only confirmed the seasonal annual migration of the bowhead, but appeared to reflect the diet consumed in these two isotopically distinct regions. Determination of minimum ages is also possible by counting the number of annual cycles exhibited in the isotopic signals. Given the fact that the WABW spends much of its life covered by ice, the ability to deduce these data from baleen is an essential tool to track its historical migratory behavior. Further information could result from examining the fine-scale patterns of fluctuation and amplitude variation in the isotopic data of

both $\delta^{18}O$ and δD. Future studies could also examine the environmental forces (i.e., sea ice concentration) driving $\delta^{18}O$ and δD variation and migratory patterns in bowhead whales. In addition, this study underscores the utility of oxygen and hydrogen isotope analyses to future studies of marine ecosystems, especially those in high latitudes. More specifically, the application of the techniques used in this study, particularly a multiple-isotope approach, could benefit investigations of trophic dynamics and the effects of global climate change on aquatic and marine community structure.

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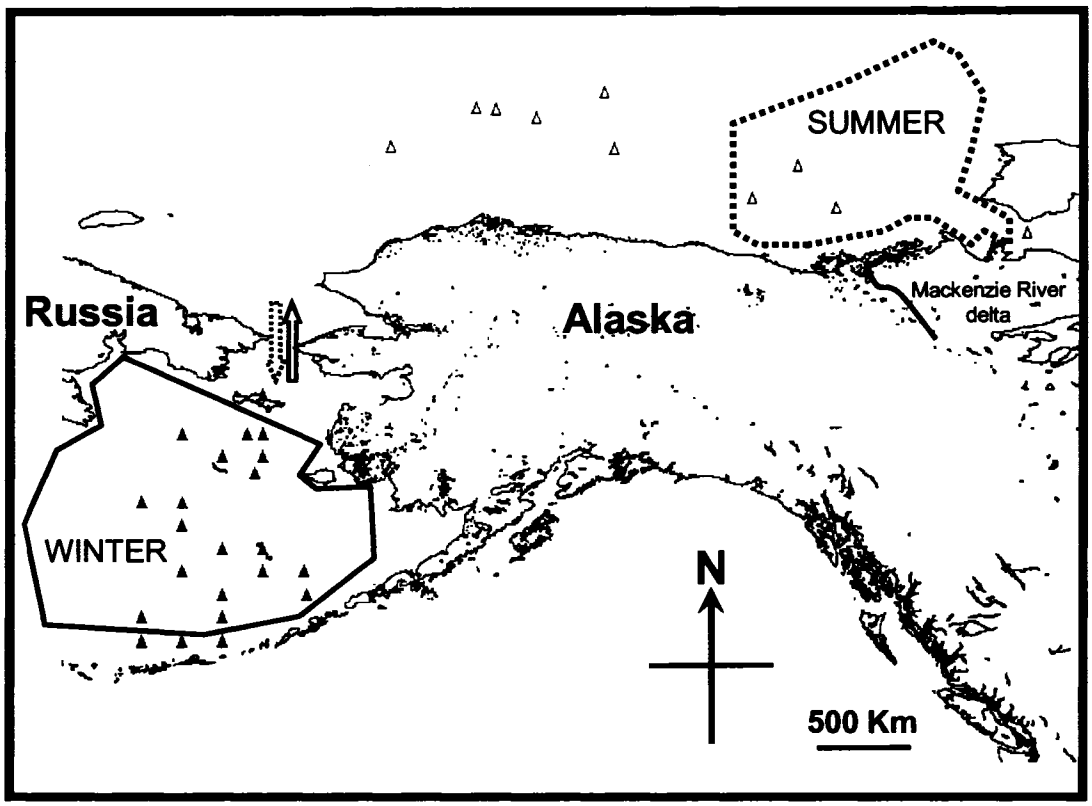

Figure 3.1. General migratory endpoints of the western arctic bowhead whales. These whales migrate north and east from the Bering Sea to the Beaufort Sea and Mackenzie River outflow region. Zooplankton sample locations are denoted from the Bering (▲) and Beaufort (Δ) seas.

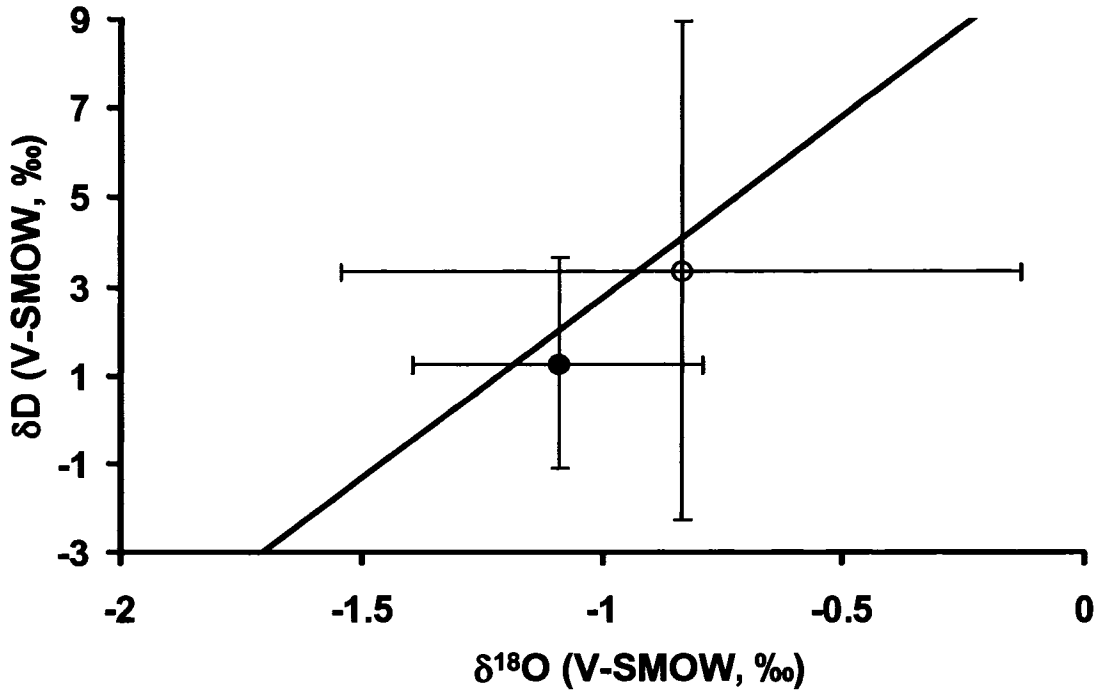

Figure 3.2. δD versus $\delta^{18}O$ of water from both the Bering Sea (•, n = 289) and Beaufort Sea (○, n = 101) ± 1 standard deviation (SD) from the NASA-GISS global seawater database and Schmidt *et al.* (1999). Mean water values from both regions follow the trend of the plotted Global Meteoric Water Line.

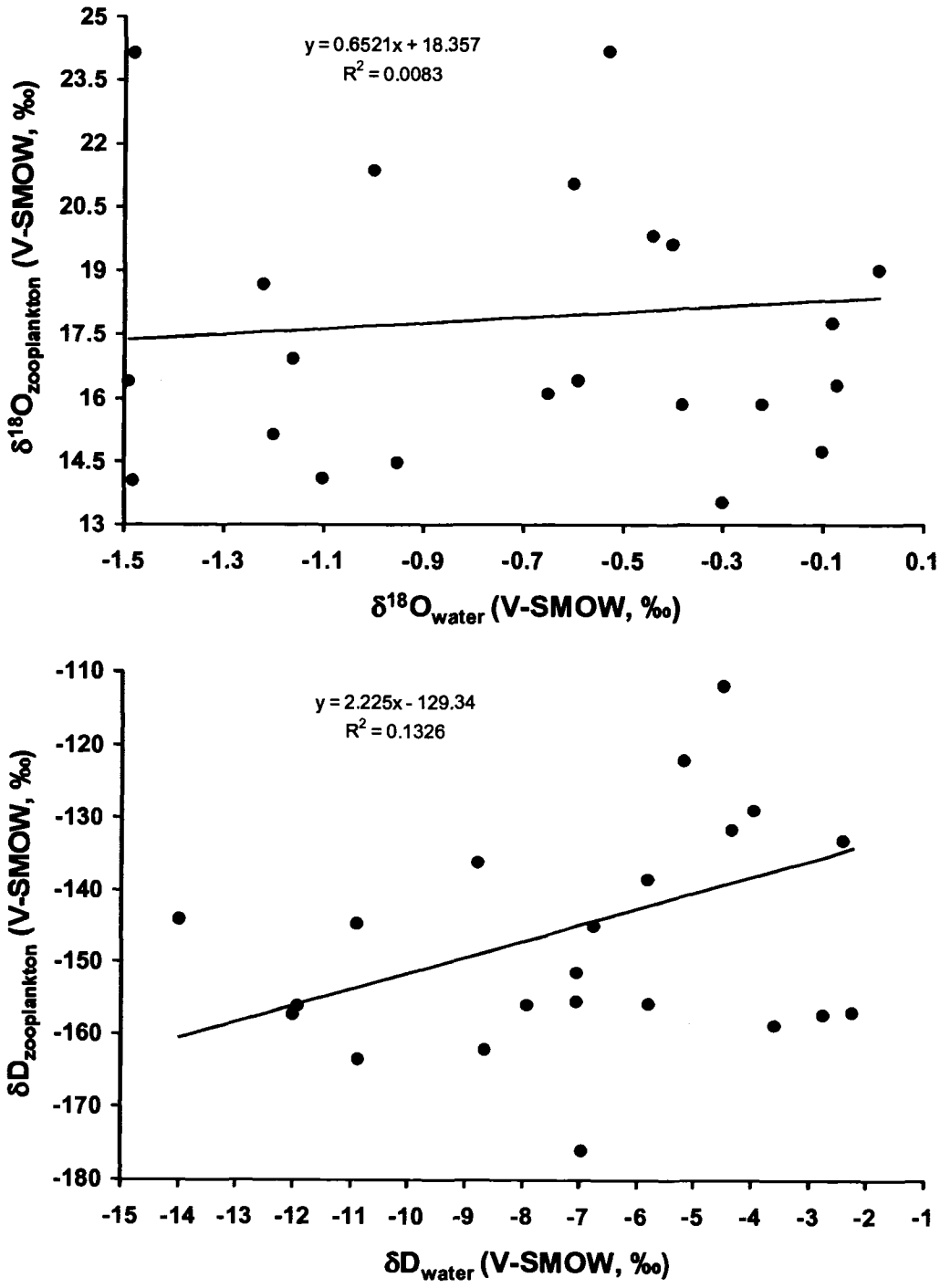

Figure 3.3. $\delta^{18}O$ (upper, p = 0.679) and δD (lower, p = 0.087) of zooplankton plotted relative to the average $\delta^{18}O$ and δD of water from the same sampling location in the Bering Sea region.

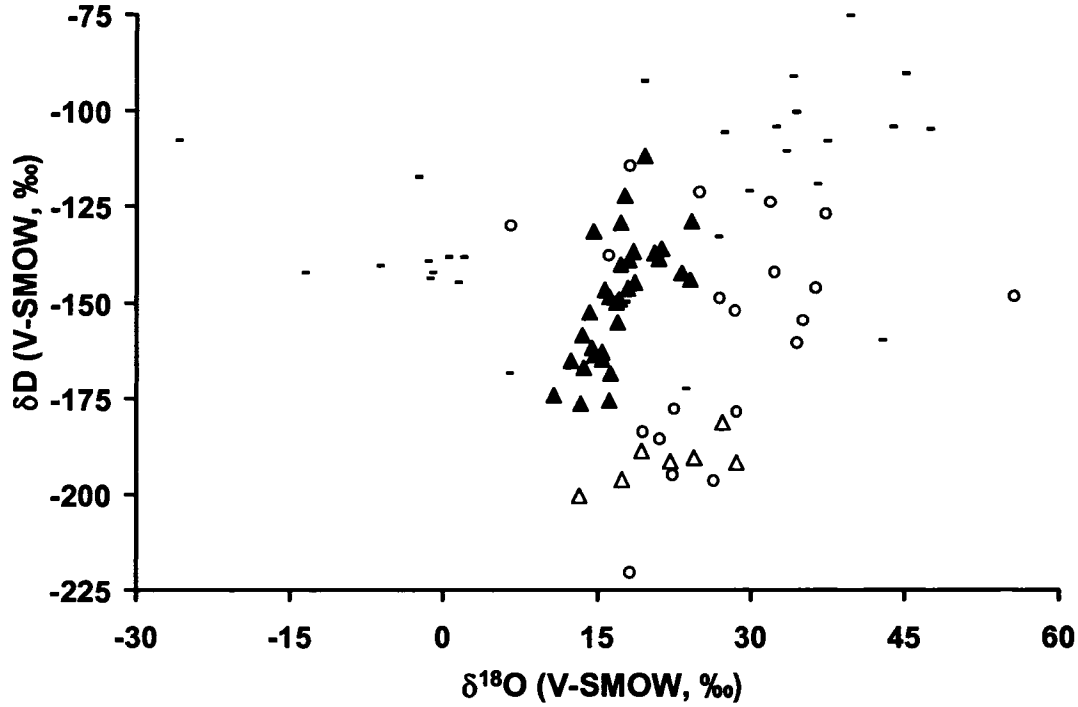

Figure 3.4. δD and $\delta^{18}O$ for all zooplankton samples. Data from the Beaufort Sea region are segregated as multiple taxa (-), only crustaceans (○), and only copepods (Δ, *Calanus hyperboreus*). Samples from the Bering Sea region (▲) are only copepods (*Calanus hyperboreus*). *C. hyperboreus* samples were isotopically indistinguishable relative to fine-scale specific regions (e.g., central Bering vs. Bering Strait and Mackenzie Bay vs. central Beaufort) from which they were sampled.

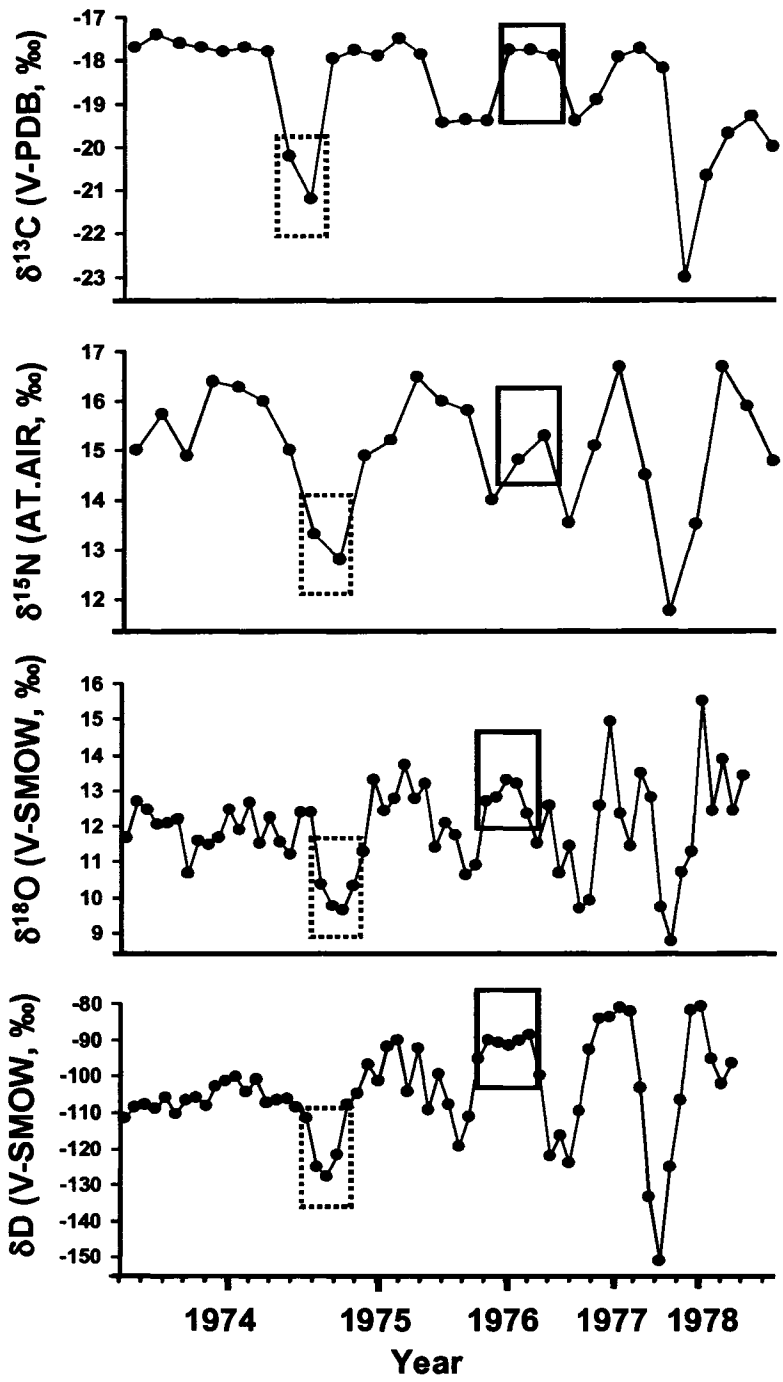

Figure 3.5. Stable isotope compositions ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, and δD) of a bowhead whale, killed off of Point Barrow, Alaska in 1978. $\delta^{13}C$ and $\delta^{15}N$ are from Schell (1992). $\delta^{18}O$ and δD values resulted from this study. Boxes are minima and maxima from the summer (dashed line) and winter (solid line), respectively. This whale was killed in spring 1978.

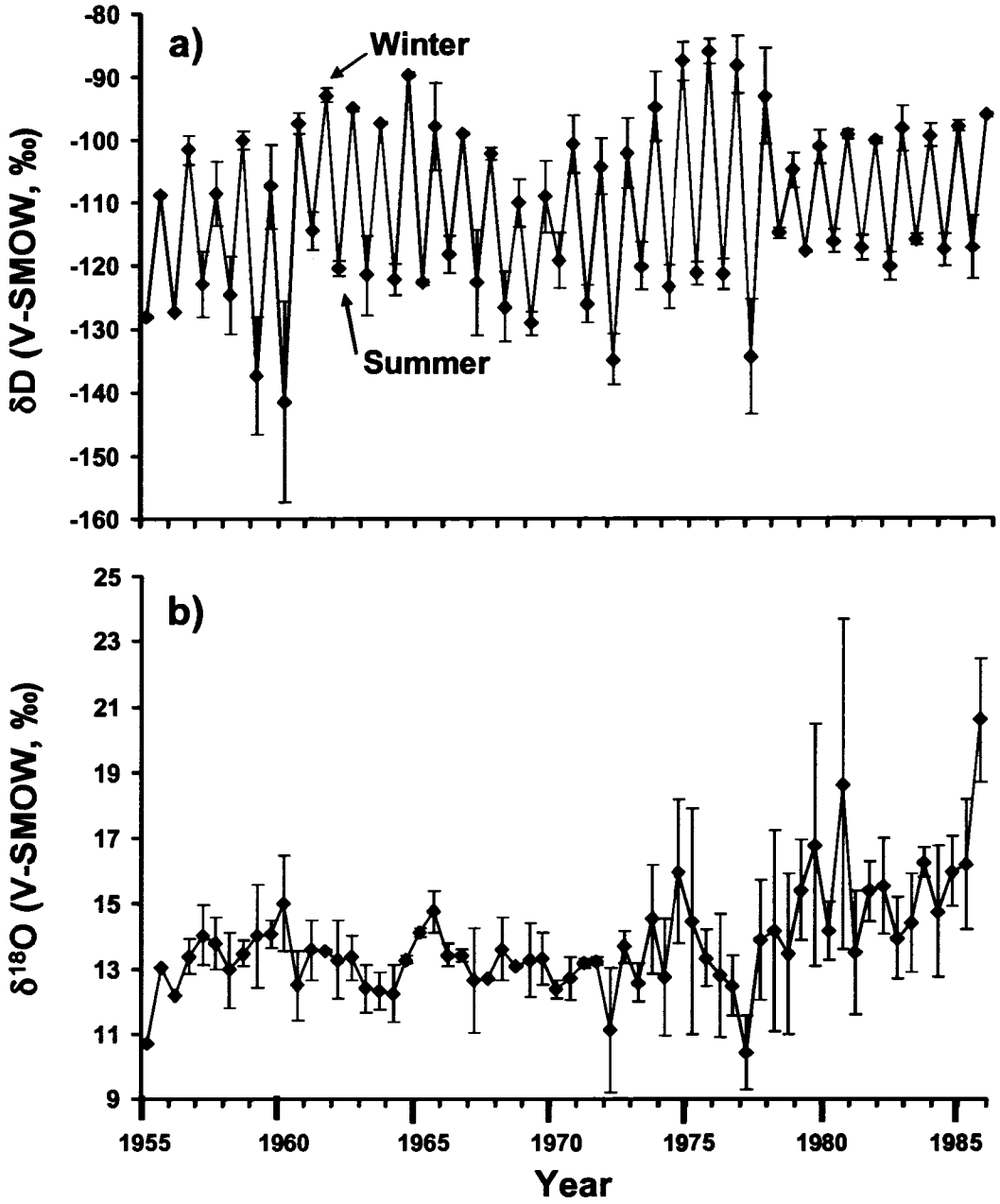

Figure 3.6. Mean δD (a) and $\delta^{18}O$ (b) (± 1 SD) of baleen samples compiled from all six bowhead whales, plotted according to each corresponding year (n = 2-3 for most years).

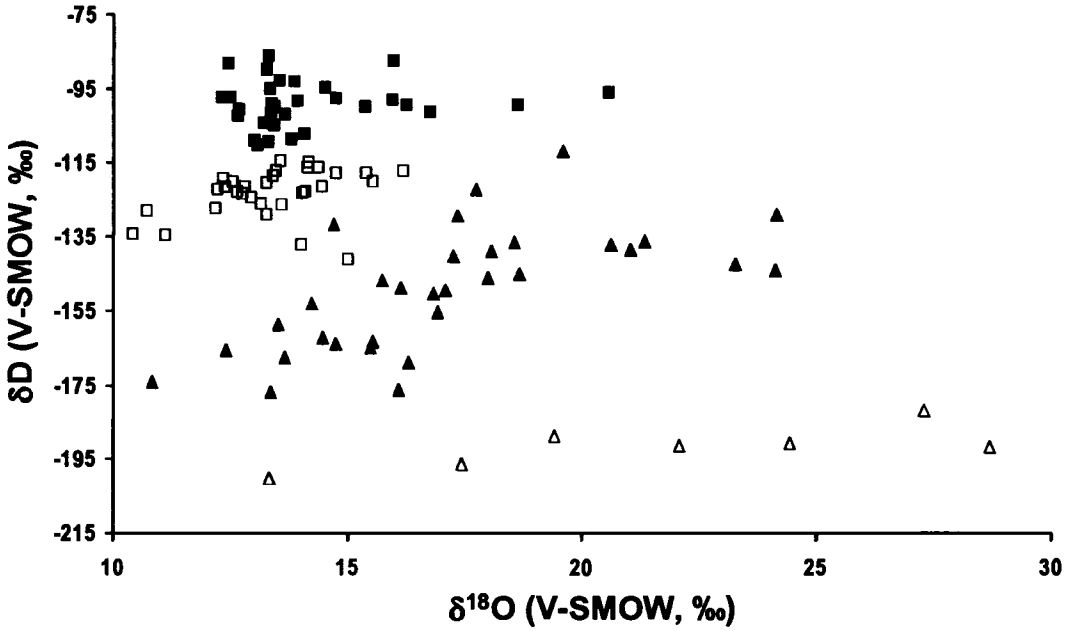

Figure 3.7. δD versus $\delta^{18}O$ of baleen from bowhead whales in the summer (□) and winter (■) and from copepods from both the Bering (▲) and Beaufort (Δ) Sea regions.

Table 3.1. The six bowhead whales, with sample code, sex, length of and years represented by the baleen, and total whale length.

Whale	Sex	Earliest Year Represented	Year of Death	Baleen Length (m)	Whale Length (m)
66-B1	Male	1957	1966	1.75	9.7
71-B1	Male	1955	1971	3.15	16
78-B1	Male	1974	1978	1.20	8.9
79-KK1	Male	1970	1979	1.88	10.6
86-KK2	Female	1966	1986	3.75	17.1
86-B3	Female	1980	1986	1.70	8.9

Table 3.2. Mean $\delta^{18}O$ and δD values (‰) for water, copepods, and whales for the Bering and Beaufort Seas, with listed p-values for the difference in each sample type between the two regions (* denotes a significant difference).

	Sample Type	Mean (± 1 SD)		p-value
		Bering	Beaufort	
$\delta^{18}O$	Water	-1.09 (0.60)	-0.83 (1.41)	0.079
	Copepods	17.13 (3.28)	21.82 (5.50)	0.073
	Whales	14.21 (1.86)	13.39 (1.34)	0.053
δD	Water	1.27 (4.80)	3.33 (11.30)	0.080
	Copepods	-149 (16.2)	-191.53 (5.85)	<0.05*
	Whales	-99.08 (6.33)	-123.15 (6.66)	<0.05*

CHAPTER 4

STABLE ISOTOPE ($\delta^{18}O$, δD) ANALYSES OF BOWHEAD WHALE BALEEN AS A BIOCHEMICAL RECORDER OF RECENT ARCTIC ENVIRONMENTAL CHANGE[3]

4.1 ABSTRACT

The marine realm of the Arctic is currently undergoing dramatic environmental changes as a result of global climate change. Changes in sea surface temperature and decreases in the extent and thickness of sea ice can have potentially drastic impacts on all levels of the ecosystem. While a number of physical and biological features are undoubtedly liable to influence the behavior of marine mammals, sea-ice concentration in particular could subsequently impact many arctic ecological communities. Western arctic bowhead whales (WABW, *Balaena mysticetus*) have a distinct seasonal migration pattern related to sea ice characteristics and it is therefore likely that the whales' migration patterns have been influenced during the recent past (1955-present) when changes in sea ice characteristics are documented. To investigate this, we analyzed the stable oxygen and hydrogen composition ($\delta^{18}O$ and δD) in the baleen plates from WABW and compared these records of WABW migration patterns with historical sea ice concentration records. WABW migration patterns appear to have altered in relation to changes in sea ice concentration over time. In years with more heavily concentrated sea

[3] deHart PAP, Picco CM, McNutt SL, Wooller MJ Stable isotope ($\delta^{18}O$, δD) analyses of bowhead whale baleen as a biochemical recorder of recent arctic environmental change. Prepared for submission to Polar Biology.

ice and colder climate regimes (e.g., 1972-1978), the difference in δD recorded in WABW baleen plates representing both winter and summer habitats was significantly greater (δD = 21.4 ± 3.6 ‰) than during warm regimes (δD = 15.2 ± 2.9 ‰) (e.g., 1979-1989). Sea ice concentration patterns can direct the habitat accessible to bowheads, and baleen may therefore be a recorder of historical sea ice concentration and climate regimes. Coupling stable isotope analyses of baleen plates with environmental variables could open the door to more effective predictions of WABW migration patterns as well as the reconstruction of past Arctic environments beyond instrumental and historical records.

Keywords: Climate change, bowhead whale, *Balaena mysticetus*, Stable isotopes, Sea ice, Migration, Global warming

4.2 INTRODUCTION

4.21 Changes in the Arctic

There has been great progress recently in monitoring and understanding the impact of climate change in the Arctic (IPCC 2001; Karl and Trenberth 2003). Large warming anomalies and shifts in sea ice characteristics and circulation patterns have been linked to changes in climate in the Bering, Beaufort, and Chukchi seas for the past 30 years (Gates 1993; Comiso 2003). The timing and extent of the seasonal (summer to winter) advance and retreat of sea ice in the Arctic and sub-Arctic can influence the annual physical and biological cycles in these areas (Alexander and Niebauer 1981; Hunt et al. 2002). Changes in sea ice are

influenced by several processes, including atmospheric forcing, from inter-annual and decadal events, to regional, short-term events such as storm track passage and associated wind forcing (Bond and Adams 2002; Overland et al. 1999; Stabeno et al. 2001). Decadal-scale changes in climate states, known as shifts in climatic regimes, can affect many levels of the ecosystem. This was particularly evident in the biological records surrounding the 1976, 1989, and 1997 climatic shifts (Fig. 4.1) (Kruse 1998; Napp and Hunt 2001; Conners et al. 2002; Overland and Stabeno 2004).

Since the 1976 regime shift, the ability of the southeastern Bering Sea shelf to support apex predators might have declined (National Research Council 1996; Napp and Hunt 2001). A shift in the Bering Sea ecosystem was particularly evident in the biological records surrounding the 1997 regime shift (Fig. 4.1). For instance, in 1997 there was a massive shearwater die off (Baduini et al. 2001), an unprecedented coccolithophore bloom (Stockwell et al. 2001), and diminished salmon returns (Kruse 1998) coincident with the climatic conditions. Some long-term changes in these ice-associated marine systems can be assessed by monitoring species at the top of the food web (Stirling 1997; Tynan and DeMaster 1997; Trites 2003). Since the Arctic and sub-Arctic are particularly sensitive to climate change (Comiso 2003; ACIA 2004) they are likely important regions to investigate the effects of climate change on marine animal behavior.

While the rate of biological adaptation to recent climate changes is unknown, it is certain that there will continue to be physical changes in temperature, precipitation, sea ice extent, and sea level rise, among other variables, if climate warming persists (Hunt et al. 2002; Karl and Trenberth 2003; ACIA 2004). These extreme transformations will likely have an

influence on the life history of biota. Researchers have already found that biota worldwide are shifting their geographic ranges or changing behaviors in ways consistent with changes occurring in their environment (Loreau et al. 2001; Kennedy 2003). The last few decades have also been characterized by a global warming trend, with warmest temperatures occurring in 2000-2004 (Overland et al. 2004). Globally, surface air temperature has increased by 0.6 °C since 1861 and the 1990s have been the warmest decade in the Northern Hemisphere. Concomitant with atmospheric changes are reductions of ice extent in the Arctic (Parkinson et al. 1999) and a decrease in ice thickness in the central Arctic (Rothrock et al. 1999). As warmer conditions and sea ice shift northward, so must the cold-region and pagophilic animal species that depend on sea ice directly as a habitat, refuge, or nursery, or indirectly for foraging. Some ice biota depend on the ice ontogenetically. For instance, species of amphipods such as *Apherusa glacialis* attach themselves to the bottom of the ice where they utilize ice algae as food, whereas allochtonous species, such as arctic cod (*Boreogadus saida*), use sea ice both to feed and as a refuge from predators (Gradinger and Bluhm 2004). Numerous additional studies document the complex biological changes that occurred throughout the arctic and sub-arctic environment in response to the warming trend and decrease in sea ice (Fig. 4.1).

Several species from the North Pacific have been documented moving north, and several northern species are moving farther northward (Overland and Stabeno 2004). Bowhead whales throughout their range select shallow inner-shelf waters during moderate and light ice conditions and deeper slope habitat in heavy ice conditions (Moore 2000; Moore et al. 2000). As the sea ice becomes less dense, bowhead whales

can migrate northward earlier or travel farther north, thereby affecting the arctic villages who depend on the whale harvest for subsistence.

The western arctic bowhead whale (WABW, *Balaena mysticetus*) is an excellent candidate to examine such effects. The WABW is a large, socially independent arctic whale with the world's longest baleen at up to over 4 m in length (Leatherwood and Reeves 1983; Braham 1984; Schell et al. 1989; Dumont and Marion 1998; Rugh and Sheldon 2002). These keratinous baleen plates grow down from the upper jaw, and are used to filter the enormous quantities of zooplankton needed to nutritionally sustain the bowhead's nearly 100,000 kg weight (Leatherwood and Reeves 1983; Lowry 1993; Rugh and Sheldon 2002). It is widely accepted that these whales follow a yearly migratory pattern (Fig. 4.2), which spans from their wintering areas in the Bering Sea north through the Bering Strait, and into the eastern Beaufort Sea (Braham 1984; Schell et al. 1988; Moore and Reeves 1993). Here, bowhead whales spend the summer in the area surrounding the outflow region of the Mackenzie River (Braham et al. 1980; Schell et al. 1984). In late summer/early autumn they migrate west, back through the Chukchi to the Bering seas (Moore and Reeves 1993; Schell et al. 1998).

These habitats traversed by the bowhead are ice-covered for much of the year, and thus the whale has evolutionarily developed the ability to break through ice up to 60 cm thick, which is evident in some of their anatomical characteristics such as their head structure and lack of dorsal fin (Leatherwood and Reeves 1983; George et al. 1989; Haldiman and Tarpley 1993; Rugh and Sheldon 2002). Bowhead whales also travel along cracks and leads along the fringes of ice floes (Dumont and Marion 1998). While the specific benefit of bowhead whale evolution in association with sea ice is unknown, and the mechanism used to detect ice

thickness has yet to be systematically identified, the bowhead whale displays behavioral characteristics consistent with the ability to detect and avoid old, thick ice areas (Dumont and Marion 1998).

Whales may be shifting their current over-wintering habitat due to both the effects of large warming anomalies on annual sea ice extent (Stirling 1997; Tynan and DeMaster 1997; ACIA 2004) as well as decreased primary productivity in the Bering Sea (Lee 2000; Schell 2000; Lee et al. 2005). If researchers are to further explore the effects of climate change on mammalian populations near the northern Bering or Beaufort seas, it is likely to require a comprehensive understanding of marine mammal migration patterns.

Changes in ice conditions due to a warming climate could affect WABW whales directly through changes in the location and abundance of their prey and/or the timing and path of their migration (Niebauer and Schell 2003). The timing and location of the sea ice during spring meltback in the Bering Sea directly affects the primary producers in the Arctic and the sub-Arctic (Alexander and Niebauer 1981; Niebauer et al. 1990; Hunt et al. 2002; Hunt and Stabeno 2002), the first link in the marine food web. For instance, early sea ice retreat can cause a decoupling between the timing and position of the spring phytoplankton bloom and the retreat of the ice edge (Niebauer et al. 1990; Alexander and Neibauer 1981). Hunt et al. (2002) hypothesized that a late season phytoplankton bloom in warmer water can occur in response to early ice retreat, creating an ideal environment for herbivorous zooplankton. An abundant zooplankton population will support a strong recruitment of forage fish, leading to an increase in predatory fish. Moreover, predatory fish compete with piscivorous marine birds and marine mammals; thus periods of warm temperature

regimes and early sea ice retreat could be detrimental to the birds and mammals in the Bering Sea (Hunt et al. 2002).

The aim of this study is to examine whether a relationship exists between WABW migration patterns and sea ice concentrations. Given that the nature of the arctic environment logistically inhibits real-time and historical tracking of migration in WABW, we use stable isotope measurements of keratin laid down temporally in bowhead whale baleen as a proxy for past WABW migration patterns. Stable isotopes have proved to be a powerful way to decipher animal migration patterns. Animals that regularly move across isotopic gradients during seasonal migrations can acquire distinct isotopic signatures along their migratory path, which can be recorded in their tissues (Deniro and Epstein 1978; Peterson and Fry 1987; Koch et al. 1989; Hobson and Welch 1992; Burton and Koch 1999; Hobson 1999; Hobson et al. 1999; Webster et al. 2002; Whitledge et al. *In press*; deHart and Wooller *In prep*). Soft tissues, such as blood and fat, are constantly regenerating; this turnover continuously alters their stable isotopic composition (DeNiro and Epstein 1978; Hobson et al. 1996; deHart 2004; deHart and Wooller *In prep*; deHart et al. *In prep*). However, some tissues are laid down incrementally (e.g., teeth, hair, nails, and feathers) and provide an isotopic record of an animal's migratory and feeding history (Schell and Saupe 1993; deHart 2004).

In the case of bowhead whales, keratinous tissue is laid down incrementally in the form of baleen plates. Recent advances in analyses of the stable oxygen and hydrogen isotope composition ($\delta^{18}O$ and δD, respectively) to track WABW migration over time (deHart and Wooller *In prep*) confirm established stable isotopic trends ($\delta^{13}C$ and $\delta^{15}N$)

that stable isotope ratios vary between winter and summer residence areas of the WABW (Schell 1998; Lee et al. 2005). Because of the historically valuable and culturally relevant nature of WABW migrations to environmental change, we use this methodology to examine long-term changes in the migration of WABW in relation to sea ice concentration.

Focusing specifically on $\delta^{18}O$ and δD variation in the Arctic and sub-Arctic, WABWs cross large stable isotope gradients (deHart and Wooller *In prep*). In northern high latitude regions there are substantial differences in $\delta^{18}O$ and δD between continental and marine systems (Kendall and Coplen 2001; Bowen and Wilkinson 2002; Bowen 2005), providing potential for enhancing our understanding of migratory behavior for animals that pass between fresh continental and marine dominated waters (Bowen et al. 2005). The $\delta^{18}O$ of continental water ranges from 3 ‰ to less than -50 ‰ and from 0 ‰ to -270 ‰ for δD (Gat 1996; Bowen and Wilkinson, 2002; Bowen et al. 2005). In particular reference to the WABW, the summer feeding grounds of this whale, the eastern Beaufort Sea and Mackenzie River drainage basin, is composed heavily by continental-derived precipitation (MacDonald et al. 1987; Gat 1996), and has lower $\delta^{18}O$ (-18 ‰) and δD (-150 ‰) relative to Standard Mean Ocean Water (SMOW, ~0 ‰ for both $\delta^{18}O$ and δD) (Schmidt et al. 1999). Recent research has shown that the migration of WABW traveling between this area of the ocean composed more heavily by continental-derived precipitation and the mean ocean water of the Bering Sea can be tracked in the keratin of their baleen (deHart and Wooller 2003, 2004, *In prep*). In this research, it was determined that $\delta^{18}O$ and δD analyses of keratin laid down in baleen plates trace WABW seasonal

migration patterns, and confirm that portions of baleen plate laid down during the time the whales are off the Mackenzie River delta (Schell 1998, 2000; Lee et al. 2005) have more negative $\delta^{18}O$ and δD values compared with those portions laid down while the animals reside in the Bering Sea (deHart and Wooller 2003; deHart and Wooller *In prep*).

4.22 Hypotheses

We hypothesized that the $\delta^{18}O$ and δD patterns from temporally overlapping but independent baleen from WABW show similar patterns, with values indicative of their seasonal habitat and corresponding to their annual migration. If this is true, it would suggest environmentally influenced migrations, and it would then seem appropriate to link environmental variables, such as sea ice concentration, to the $\delta^{18}O$ and δD data. The $\delta^{18}O$ and δD of baleen plates should display disparate patterns, given the trends observed by deHart and Wooller (*In prep*), with δD signatures displaying the seasonal migratory cycles more clearly than $\delta^{18}O$. The magnitude of difference (‰) in the $\delta^{18}O$ and δD between continental and ocean water is much greater in δD than $\delta^{18}O$ (Kendall and Coplen 2001; Bowen and Wilkinson 2002; Bowen 2005), so should be more pronounced in animal tissues as well (Hobson et al. 1999; Bowen et al. 2005).

Given the limitations that the extent and density of sea ice could place on regulating the migration pattern of WABW, we hypothesized that there should be a correlation between past WABW migration patterns and the historical sea ice concentration data covering the same time period. In terms of WABW, we hypothesized that their migration has been influenced by both sea ice extent and density. On the basis

of this rationale, we examined the relationship between WABW migration and sea ice concentration. Sea ice concentration is defined here as "the percentage of ice-covered surfaces within the satellite footprint or grid, while the ice extent is the sum of the area of all data elements which has at least 15% sea ice concentration" (Thomas and Dieckmann 2003). The satellite footprint grid, which varies between studies depending upon the satellite used, refers to the pixel size, which was 0.25° x 0.25° in this study (Picco 2005). The data elements refer to the compilation of all elements (e.g., aerial photos, satellites, etc.) incorporated (Thomas and Dieckmann 2003). In this study, the data element utilized was solely satellite data (Picco 2005). Satellite-derived sea ice concentration data for the Bering Sea from 1972-2000 should provide new insight into ice conditions in the marginal ice zone of the Bering Sea, and can be used to demonstrate the effects of physical forcing on the sea ice from seasonal to decadal timescales (Alexander and Niebauer 1981; Neibauer et al. 1990; Clement et al. 2004; Picco 2005).

Following the conclusions of Stabeno et al. (2001) maximum sea ice extent alone does not account for the regional variability in the sea ice cover. Using sea ice concentration, which accounts for ice extent, gives a new variable for analysis of sea ice dynamics. In years of low sea ice concentration, more enriched $\delta^{18}O$ and δD values (closer to 0 ‰) should be observed in WABW baleen plates. This is due to whales feeding further from isotopically depleted freshwater inputs (Mackenzie River) and more in the realm of mean ocean water, with much lower $\delta^{18}O$ and δD compared to SMOW. Years of low sea ice concentration would allow WABW passage to areas further from Mackenzie River delta during summer. Conversely, we expect greater ice concentration

during cold climate regimes (e.g., 1972-1977) than warm (e.g., 1977-1989) (Stabeno et al. 2001). Colder climate could yield thicker and more expansive ice sheets (Overland and Pease 1982; Parkinson et al. 1999; Overland et al. 2004), forcing whales further into the ocean water of the Bering Sea throughout the winter, and closer to shore and the freshwater outflow regions of the Mackenzie Bay in the summer months; this should be displayed as greater variation between seasons in the isotopes of the baleen (i.e., a greater difference between the $\delta^{18}O$ and δD from baleen laid down in the summer compared with that during winter).

4.3 MATERIALS AND METHODS

4.31 Stable oxygen and hydrogen isotope analyses

We analyzed archived (at the Alaska stable Isotope Facility, ASIF) samples from fourteen baleen plates compiled by D. Schell and collected from a joint effort of NOAA-NMFS, Alaska Native Subsistence Hunters, the North Slope Borough Department of Wildlife Management, the Los Angeles county Museum, and the Alaska Dept. of Fish and Game. Supporting data were available prior to the analysis of these samples, including age, size, sex, condition, and location of death (Schell 2000). Samples were taken at 2-5 cm intervals along the whole length of the baleen. These keratinous tissue samples provide a temporal record of whale migration over the whole of the animal's life and in total represent a 33-year period spanning from 1955 to 1988. By overlapping the records from whales killed in different years, a continuous temporal record was constructed. Visual matching of minima for each baleen was conducted in concordance with the protocol previously established by Schell et al. (1988).

The finely powdered, dried, and homogenous baleen was weighed into tin capsules (3 x 3 mm; approximately 0.3 mg powder) that were each subsequently crimped shut. These samples were analyzed using a Thermo Finnigan Delta^{plus}XL stable isotope ratio mass spectrometer (IRMS). This instrument was interfaced via a Finnigan Conflo III with a Thermoquest high temperature conversion elemental analyzer (TC/EA). Each sample was pyrolyzed into H_2 and CO gases that were then separated chromatographically. These gases were then conveyed to the IRMS with a continuous flow of Helium carrier gas. The stable isotope ratios obtained are expressed in standard delta (δ) notation, as parts per thousand (‰). Stable isotope ratios were expressed as:

$\delta^{18}O$ or $\delta D = [(R_{sample}/R_{standard})-1] \times 1{,}000$

where R_{sample} and $R_{standard}$ are the ratios of $^{18}O/^{16}O$ or $^{2}H/H$ for the sample and standard, respectively.

δD and $\delta^{18}O$ values are reported relative to Vienna Standard Mean Ocean Water (V-SMOW). For quality control, empty tin capsules were analyzed every twenty samples and working standards (benzoic acid [Fisher scientific, Lot No. 947459]) were analyzed every ten samples. Analytical precision based on the standard deviation of benzoic acid reference checks for $\delta^{18}O$ and δD ranged from 0.1 to 1.1 ‰ for oxygen and 1.0 to 8.4 ‰ for hydrogen. The % oxygen precision ranged from 0.4 to 0.8, while % hydrogen precision ranged from 0.1 to 1.3. Each entire run was calibrated relative to a calibrated WABW baleen standard (BWBII- see Hobson et al. 1999), as well as the National Institute of Standards and Technology (NIST) standards NBS-19, NBS-22, NBS-30,

PEF-1, and sucrose ANU, which formed a calibration curve with an r^2 of >0.99. Data are expressed throughout as mean ± 1 standard deviation (SD).

For similar studies analyzing δD of organic substances (e.g., keratin), issues related to hydrogen exchange have been described by others (e.g., Wassenaar and Hobson 2002). We therefore adopted a protocol consistent with that outlined by Wassenaar and Hobson (2002) where samples and a calibrated keratin standard (BWBII; calibrated δD = -108.2 ‰; Hobson et al. 1999) were "air-equilibrated" with ambient laboratory air moisture in ASIF at room temperature for more than 96 hours prior to δD analysis. After more than 96 hours of equilibration, all samples and standards were loaded into the autosampler of the TC/EA-IRMS. The δD of sample hydrogen was calculated by measurement of HD isotopes (after standard H^{3+} corrections) and comparison to a pulse of monitoring H_2 gas (research grade 99.99 %; V-SMOW). Analysis of BWBII yielded a δD of -109.1 ‰. The ‰ difference (0.9 ‰) between this value for BWBII and its calibrated value (-108.2 ‰; Hobson et al. 1999) is consistent with the lower range of our δD analytical precision (1.0 ‰).

4.32 Baleen temporal data

To obtain replicate samples for temporal analysis, multiple techniques were used to ensure the data obtained was in fact representative of the season and year implied. We initially used temporal data of Schell (2000) and followed the protocol established by Schell and Saupe (1993) with specific distances from the base to distal tip corresponding with a specific calibrated radiocarbon age. Since we obtained higher temporal resolution

in our study and to ensure accuracy of our calculated years, we additionally visually matched our cyclical $\delta^{18}O$ and δD data with the established $\delta^{13}C$ and $\delta^{15}N$ patterns (e.g., as in deHart and Wooller *In prep*) for each whale baleen to determine the annual points of temporal overlap. This gave us a season and year for each series of data points, and each maxima and minima along the length of a baleen. For composite analysis, we then calculated the mean (± 1 SD) for each temporal span, using the maximum or minimum (winter or summer, respectively) of each baleen as being representative of the season for each particular year. For each time point (i.e., a winter and summer data point for each year), sufficient overlap was present from having run all 14 WABW to allow an n of ≥ 6 individual whales in most instances (we draw attention to where this was not possible in our results section). A difference in δD was calculated as the absolute value of the difference (‰) between the composite mean winter and summer δD for each given year.

4.33 Sea ice concentration data

The trends in $\delta^{18}O$ and δD in the baleen of WABW are compared to historical sea ice concentration, temperature trends, and environmental variable records derived from Picco (2005). Following the established protocol of Picco (2005), satellite-derived data from 1972-2000 were analyzed for the Bering Sea and sea ice concentration and are reported as average anomalies in tenths (10^{th}s) of 10 gradations of concentration coverage per year. Spatial differences were analyzed for each year overlapping with the whale stable isotopic dataset (1972-1988), and grouped into years respectively based on

accepted climatic regime shifts: 1972-1976 (cold) and 1977-1988 (warm) for further analysis (e.g., Stabeno et al. 2001).

4.34 Data analysis

Stable isotope data are expressed throughout as means (± 1 SD) across whale samples per unit time (e.g., summer and winter per year). We used one-way ANOVAs to compare the two isotopes, seasonally segregated, to sea ice concentration both throughout the whole study period and temporally separated for the two climate regimes (cold 1972-1977, and warm 1977-1988). T-tests were used to determine equivalence of means, and F-tests were used to determine consistency in variance between mean isotopic values of each season in the whale baleen, as well as for a seasonal comparison of the difference between seasons with both $\delta^{18}O$ and δD. Significance was tested at the $\alpha = 0.05$ level.

4.4 RESULTS

The $\delta^{18}O$ and δD values in all whale samples corresponded to the annual migration of WABWs, but the average isotopic signatures per year for all whales display different patterns between the $\delta^{18}O$ and δD (Fig. 4.3). While the yearly mean of δD did not change significantly over the study period ($R^2 = 0.01$, $p = 0.411$), there was a net change of ~8 ‰ in the mean $\delta^{18}O$ from 1955 to 1988 ($y = 0.061x + 12.375$, $R^2 = 0.592$, $p < 0.05$) with a larger increase in mean $\delta^{18}O$ from 1976 to 1988 (Fig. 4.3b). This change is observed in both the summer and winter month peak averages. There is an observed

cyclical seasonal signature in $\delta^{18}O$ and δD for all whales (Fig. 4.3), and δD signatures (Fig. 4.3a) seem to display the seasonal migratory cycles more clearly than $\delta^{18}O$ (Fig. 4.3b). There was a significant difference between the mean δD values for all whales between the summer (Beaufort Sea) and winter (Bering Sea), but not for $\delta^{18}O$ (Table 4.1).

Sea ice concentration in the Bering Sea decreased with year from an average 4.25 10^{th}s in 1972 to 3.5 10^{th}s at the end of the study period in 2000 ($p<0.05$; Fig. 4.4). An abrupt change in sea ice concentration occurred in 1976-1978, where the highest sea ice concentrations occurred from 1976-1977 followed by a subsequent sea ice response yielding the third lowest sea ice concentrations in the study period by 1978.

Comparing the δD and $\delta^{18}O$ values by season in relation to the sea ice concentration values, we observed different trends between the two stable isotopes (Fig. 4.5). Concomitant with increasing sea ice concentration there is a net increase in δD in winter with a simultaneous decrease or no change observed in δD during summer (a greater difference between the two seasons with increasing sea ice concentration) (Fig. 4.5a). For $\delta^{18}O$, however, there is little difference between means of the two seasons, as both remain relatively constant with changing sea ice concentration (Fig. 4.5b).

Given these results, we more closely examined the correlation between the difference in average δD and $\delta^{18}O$ between the two seasons for each year to the changes in sea ice concentration with time, between the years 1972 and 1988. An initial view of these two variables plotted over time yielded a correlation between the difference between season for δD and the temporal patterns in sea ice concentration (Fig. 4.6). The correlation between the two resulted in a statistically significant relationship between sea

ice concentration and difference in δD between seasons (Pearson coefficient = 0.536, $p<0.05$), whereas $\delta^{18}O$ showed no such significant correlation (Pearson coefficient = 0.069, $p = 0.70$). A regression analysis of difference in δD with sea ice concentration further elucidated this result, as with increased sea ice concentration there was a greater variation between the seasons in δD (Fig. 4.7; $p<0.05$).

The mean and variance of the seasonal difference in δD values differed significantly between the two climate regimes during the time period between 1972 and 1988 (mean difference in δD: cold = 21.4 ± 3.6 ‰, warm = 15.2 ± 2.9 ‰; $F_{[1,15]} = 14.79$, $p <0.05$). This was not the case with the seasonal difference in $\delta^{18}O$ values, which showed no significant difference between climate regimes (mean difference in $\delta^{18}O$: cold = 0.7 ± 0.4 ‰, warm = 0.5 ± 0.5 ‰; $F_{[1,15]} = 0.21$, $p = 0.66$). The winter season δD values followed the identical patterns of the overall difference in δD, with the cold regime significantly lower relative to the warm regime (mean δD: cold = -98.3 ± 4.2 ‰, warm = -103.8 ± 3.0 ‰; $F_{[1,15]} = 10.04$, $p <0.05$). There was no difference observed between the climate regimes for the summer season in δD and both seasons in $\delta^{18}O$.

4.5 DISCUSSION

4.51 Bowhead whale migration

The $\delta^{18}O$ and δD patterns from temporally overlapping but independent WABWs show similar patterns, with values indicative of their seasonal habitat and corresponding to their annual migration. This result, in context of the independent and solitary migratory

behavior of the WABW, seems to suggest that patterns in the arctic and sub-arctic environment were influencing their migrations. Given this result, we found it appropriate to examine whether a relationship existed between these isotope data and an environmental variable, sea ice concentration. The $\delta^{18}O$ and δD values displayed disparate patterns, and followed the same manner as observed by deHart and Wooller (*In prep*). The δD signatures display the seasonal migratory cycles more clearly than $\delta^{18}O$, and the patterns we observe are likely a reflection of the WABW migrations. The increase in $\delta^{18}O$ over time (Fig. 4.3b) confirms the trends suggested by deHart and Wooller (*In prep*), and may indeed be driven by another mechanism, such as long-term temperature increases (IPCC 2001, Karl and Trenberth 2003, ACIA 2004) or variations in the phytoplankton record similar to what has been seen in terrestrial plants (Sternberg et al. 1986b, McCarroll and Loader 2004).

Our hypothesis that the $\delta^{18}O$ and δD from WABW baleen is environmental in origin and not simply due to physiological responses or behavioral patterns in individual whales is supported by the close agreement in isotopic ratios between multiple whales ($n > 6$ for each data point, with minimal exception; Fig. 4.3), regardless of whale age or baleen length, for a given year (Fig. 4.3a). These results are similar to what was found with $\delta^{13}C$ analyses of the same baleen plates (Schell 2000). The whales appear to be obtaining this lower δD and $\delta^{18}O$ directly from the zooplankton prey of the Beaufort Sea and Mackenzie Bay region, where these whales spend the summer feeding (deHart and Wooller *In prep*).

4.52 Sea ice concentration and isotopic data

In the analysis of the satellite-derived sea ice concentration data for the Bering Sea from 1972-2000, we observed a net decrease in sea ice concentration over the period from 1972-2000, as well as separately in the time overlapping that of the WABW baleen data (1972-1988). Given this result, it is clear that concentration data correspond to prior trends established for extent and thickness (Gates 1993; Tynan and Demaster 1997; IPCC 2002; Comiso 2003), and would therefore seem to be the most appropriate sea ice variable to compare the WABW migration patterns. In years of low sea ice concentration, higher δD values were observed, which is likely due to whales feeding further from isotopically depleted freshwater inputs and more in the realm of mean ocean water. The $\delta^{18}O$ and δD, however, display different patterns with this respect (Fig. 4.5). While δD is strongly correlated with sea ice concentration (Fig. 4.6), there is little difference in $\delta^{18}O$ between mean values of the two seasons, with both winter and summer remaining relatively constant with changing sea ice concentration (Fig. 4.5b). This might be due to the relatively small magnitude of $\delta^{18}O$ naturally occurring in both the environment (e.g., water and prey. deHart and Wooller *In prep*) and the whales relative to δD.

These findings imply that baleen δD could be used as a proxy for sea ice/climate patterns. Conversely, the correlation between the difference in δD between seasons and sea ice concentration could allow for future sea ice patterns from satellite data to be used to predict whale migrations and guide management protocols in the western Arctic. The abrupt change in sea ice concentration that occurred in 1976-1978, where the highest sea

ice concentrations occurred from 1976-1977 followed by the third lowest ice concentrations in the study period by 1978, highlights the innate extreme nature and variability of this ocean system. There indeed appears to have been greater sea ice concentration during cold climate regimes than warm regimes, yielding thicker and more expansive ice sheets (Picco 2005). This increase in sea ice concentration is concomitant with the increased difference in the δD signature between seasons evident in the WABW baleen. This increase in sea ice concentration during cold climate regimes likely forced whales further into ocean water in the Bering Sea throughout the winter, and closer to shore and the freshwater outflow regions of the Mackenzie Bay in the summer months. This might suggest that climate is a significant driving force in the migration of WABW; perhaps more so than regional changes in primary productivity with time. The $\delta^{15}N$ and $\delta^{13}C$ data for the WABW we examined indicated that no major shift in trophic status in the whales occurred during this time (Schell 2000). Given this, another potential cause for the shift in δD include a systematic shift in feeding habitat of the whale to regions of higher average δD in prey (further from freshwater outflow regions) corresponding with increased sea ice concentration.

Picco (2005) determined that sea ice was decreasing faster and was more variable in the southern and eastern Bering Sea regions than in the northern and western regions. These findings agree with Luchin et al. (2002) who found a statistically insignificant tendency towards warming in the northern regions. The difference in sea ice concentration between the east and the west could be due to the larger area of shallow continental shelf in the eastern Bering Sea (Stabeno et al. 2001). The continental shelf

reaches latitudes of almost 54° in the east and 60° in the west and the sea ice does not typically extend further than the shelf over the long term (Overland and Pease 1982). The further south the ice edge extends, as in the east, the more susceptible it will be to the warmer inflow of water from the North Pacific, potentially causing a faster rate of decline in sea ice concentration over time (Stabeno et al. 1999). While Schell (2000) discounted the likelihood of WABW utilizing the eastern Bering Sea for habitat and migration, there has subsequently been further evidence suggesting that this is a region well-used by these whales (Moore et al. 2002). There is, as well, evidence for patterns of geographically distinct and segregated sea ice changes within the Bering Sea (Picco 2005), that could direct whale habitat selection. Variations in sea ice concentration correspond with δD changes from this study, suggesting that WABW do indeed potentially utilize the eastern Bering Sea region for overwintering. The changes observed could be due to WABW following the changing edge of the sea ice, and the results of this study cast doubt on the conclusion that changes in whale feeding patterns (derived from $\delta^{13}C$ measurements of the same baleen plates) are due solely to declining carrying capacity in the Bering Sea (Schell 2000, 2001). Rather, it seems likely that the changes in WABW foraging are likely driven by large-scale shifts in climate and sea ice concentration.

Looking more closely at environmental changes in specific temporal periods, it is generally accepted that a regime shift occurred in 1976-1977 (Francis and Hare 1994; Steele 1998; Hare and Mantua 2000). Less intense shifts occurred in 1989-1990 (Hare and Mantua 2000) and in 1996-1997 (Stabeno et al. 2001). Sea ice concentration data used in this study show evidence of response to regime change, with the most recent

changes closely linked to sea ice (Fig. 4.2) (Picco 2005). Our results show that an abrupt change in sea ice concentration lagged the regime shift in 1976-1977 by one year. The highest ice concentrations during this study occurred from 1976-1977. One year after this regime shift in 1978, the ice responded with the third lowest ice concentrations in the study period. The decades of cold, stable ice years, cold sea surface, and bottom temperatures leading up to 1976 (Francis et al. 1998; Polyakov et al. 2003) could have buffered the response of the sea ice to the regime shift in the 1970's (Picco 2005). The cumulative affect of the climatic variables on the sea ice concentration over time was more significant than when years were analyzed individually. Spring ice conditions are more variable and there is also evidence of earlier meltback. The sea ice concentration in the Bering Sea showed an overall decrease from 1972-2000. This decrease exhibited regional patterns with southern and eastern regions decreasing at a faster rate than northern and western regions, respectively. Overall, the sea ice concentration has been decreasing on average since 1986-1987.

The sea ice records in this study support the concept that a major climatic event occurred in 1989-1990 (Hare and Mantua 2000; Picco 2005) and that this also influenced the WABW migration. The Bering Sea experienced the lowest ice concentrations of all years in 1989-1990, while in 1997, the ice responded with the second lowest spring ice concentration in the 28 year study period. Parkinson et al. (1999) found that 1996 had the lowest yearly ice average. Unlike the regime shift of the 1970's, the sea ice concentration of the late 1980's and 1990's decreased immediately in response to their respective regime shifts. Future studies could examine the trends of δD from baleen over

this proposed additional climatic event. Given the results of this study, we speculate that the overall difference in δD between seasons decreased during this warm period (Fig. 4.6). With a continuing warming trend and decrease in ice concentration, sea ice could become less stable and more responsive to large-scale regime shifts.

Given the relationship between seasonal difference in δD of WABW baleen and sea ice concentration (Figs. 6, 7), we could predict the δD trends resulting from further analyses of WABW baleen covering additional recently documented regimes from 1990-1997 (cool, "Regime 3") and 1998-2000 (warm, "Regime 4") (Parkinson et al. 1999; Stabeno et al. 2001; Picco 2005). If the patterns we have established are consistent, given that Regime 3 had equal average ice concentration to Regime 2 (warm, 1979-1989), the difference in δD between 1990 and 1997 should be equivalent to the 10 years prior, but not as great as the more extreme "cold" regime (#1) from 1972-1978 (Picco 2005). Since Regime 4 had the lowest average sea ice concentration, that possibly extends out to 2004 (Clement et al. 2004; Overland and Stabeno 2004; Picco 2005), then less variation in the δD of baleen between seasons should be observed during this time period.

Recent work pairing visual sighting and sea ice extent (Moore 2000; Moore et al. 2000) suggests that, while bowheads are pagophilic mammals, they may not be as closely associated with ice as has been proposed by some researchers (e.g., Stirling 1997). Observing the extent of sea ice in summer months, Moore (2000) concluded that bowheads select coastal waters in light ice years and outer shelf and slope waters in heavy ice years. Moore et al. (2000) also indicated that, rather than physical forcing from sea ice patterns, changes in oceanographic patterns likely drive WABW seasonal

distribution. Extrapolating our results to this particular temporal period, however, suggest that if the patterns in δD are consistent, WABW likely migrated between their two seasonal regions further from shore (i.e., closer to mean ocean water), and remained further from freshwater outflow areas between 1998 and 2004 (Fig. 4.8). While we certainly cannot discount influences of altered fine-scale ocean circulation patterns and prey distribution on habitat selection of the WABW, this study indicates that physical forcing and sea ice concentration likely influence WABW migrations as well. This trend is confirmed in accounts of traditional ecological knowledge (Krupnik and Jolly 2002). The discrepancy between these divergent claims is likely due to methodology, as sea ice extent does not take into account the ice concentration variable (Picco 2005). Given the life history characteristics of the WABW and its ability to and common behavioral patterns of breaking through thin ice (Leatherwood and Reeves 1983; George et al. 1989; Dumont and Marion 1998; Rugh and Sheldon 2002), sea ice extent is less likely to drive habitat selection and migration of the WABW than the composite proxy of sea ice concentration (Picco 2005).

The patterns in the overall seasonal difference in δD for all years represented in the baleen, including dates prior to the start of the sea ice concentration record in 1972 (Fig. 4.8), correspond to what is expected from the historical temperature and sea ice extent record for this region (Chapman and Walsh 1993; Serreze et al. 2000; Johannessen et al. 2004). As confirmed from the δD patterns observed between 1955 and 1972, the climate of the western Arctic on the whole was cooler prior to 1972, with two possible small warm regimes interspersed. In addition, as opposed to Regime 3 in the 1990's, the

years prior to 1972 were likely defined as "cold", displaying the highest difference in δD in the past fifty years between 1960 and 1965 (Fig. 4.8). This suggested cold period as seen from the δD patterns is supported by the observed temperature record for this region, with the coldest temperatures between 1955 and 1988 occurring in the early 1960s (Johannesson 2004). It is therefore likely that the sea ice concentration was highest in the past half century from 1960 to 1965. Future efforts should be made to confirm these historical estimations to sea ice concentration through overlap of additional baleen, and using the relationships between climate regime and seasonal difference in δD established in this study.

4.6 SUMMARY AND CONCLUSIONS

The correlation between the seasonal difference in δD and climate regime illustrates a potential for reconstructing past sea ice concentration by examining the difference in δD in baleen dating back beyond the sea ice record (Fig. 4.8). Utilized in conjunction with additional cutting-edge examinations of past environments (e.g., ice and ocean sediment cores; ACIA 2004), including additional isotopic examinations (Hobson 1999; Schell 2000, 2001; Hirons et al. 2001; Bowen et al. 2005), analysis of δD patterns could elucidate historical climate characteristics. We may also be able to use these patterns to make suggestions as to the trends of past climate regimes. From the δD patterns observed prior to 1972, we suggest that the cooler climate during this period is evident in the baleen of whales, which was likely driven by higher ice concentration. The relationships between climate regime and seasonal difference in δD could be modeled in

relation to additional environmental temperature indicators for this region (i.e., sea ice extent).

Additional forms of evidence to support long-term changes in climate have been building (see IPCC 2001; ACIA 2004), and it is clear that, while the sea ice record only extends back 40 years, the observed warming in the Arctic in the past 100 years has no precedent since the early Holocene (IPCC 2001; Mann and Jones 2003). While it is feasible to confirm the existence of a greater sea ice extent from this past cooler climate, there has been a call to further quantify such changes in a specific manner to fill in such an observational gap as the historical sea ice record (ACIA 2004). In addition, it is clear that there is a need to develop long-term biological time series in the Arctic, as it is essential to document and interpret the effects of global warming on polar ecosystems (Tynan and DeMaster 1997). Examining δD patterns in historical WABW baleen and using them to reconstruct past foraging behavior and forcing factors such as sea ice concentrations in the Bering Sea, Chukchi Sea, and Arctic Ocean could fit this need.

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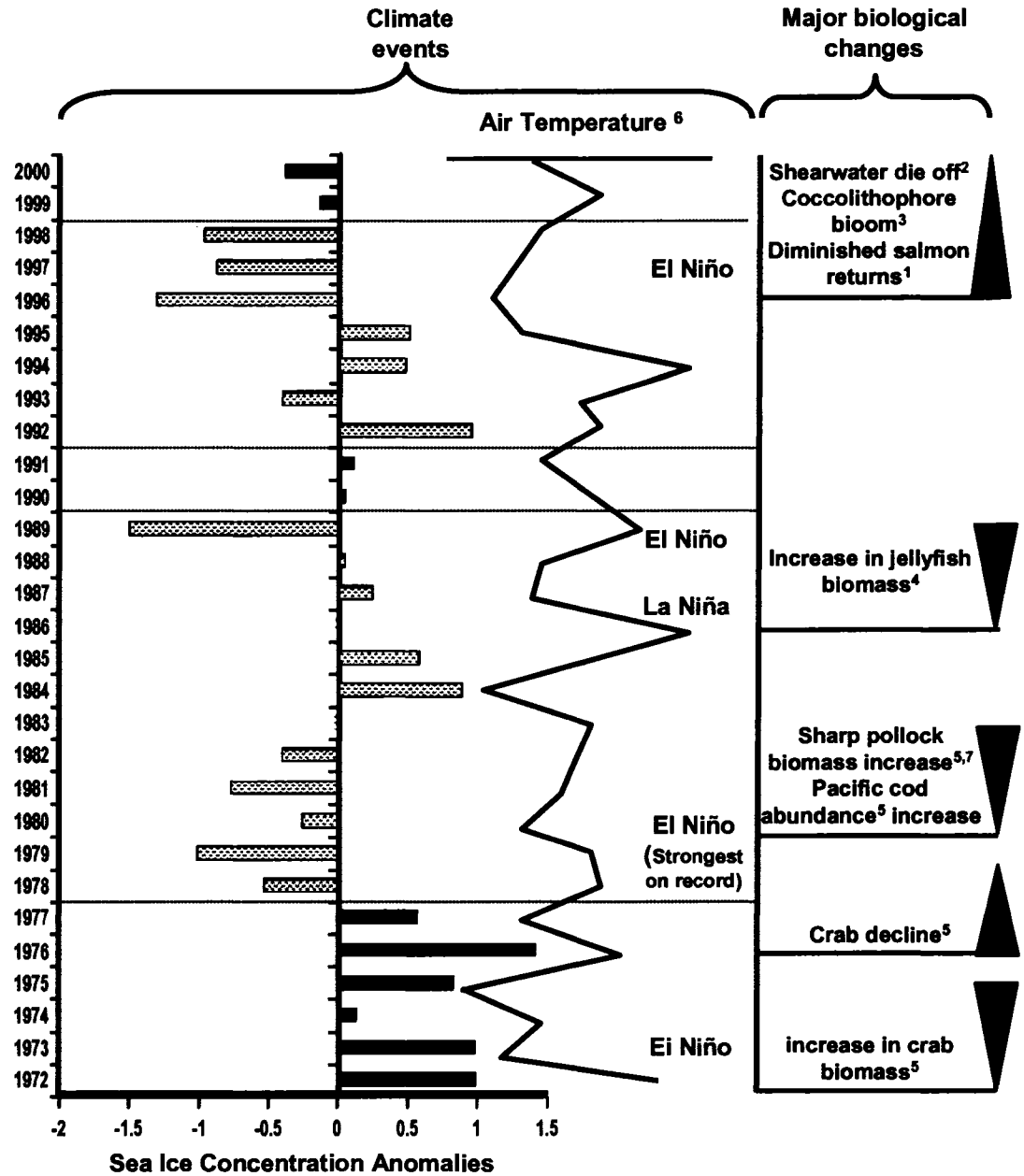

Figure 4.1. Some of the changes in the Bering Sea ecosystem from 1972-2000, including indicators of climate, sea ice concentration, temperature, climate events, and biological shifts ([1]Kruse 1998; [2]Baduini et al. 2001; [3]Stockwell et al. 2001; [4]Brodeur et al. 2002; [5]Conners et al. 2002; [6]Polyakov et al. 2003; [7]Overland and Stabeno 2004). Average Pacific Decadal Oscillation phases: cold (solid bars) and warm (hatched bars), with transitions between regimes highlighted by dotted lines.

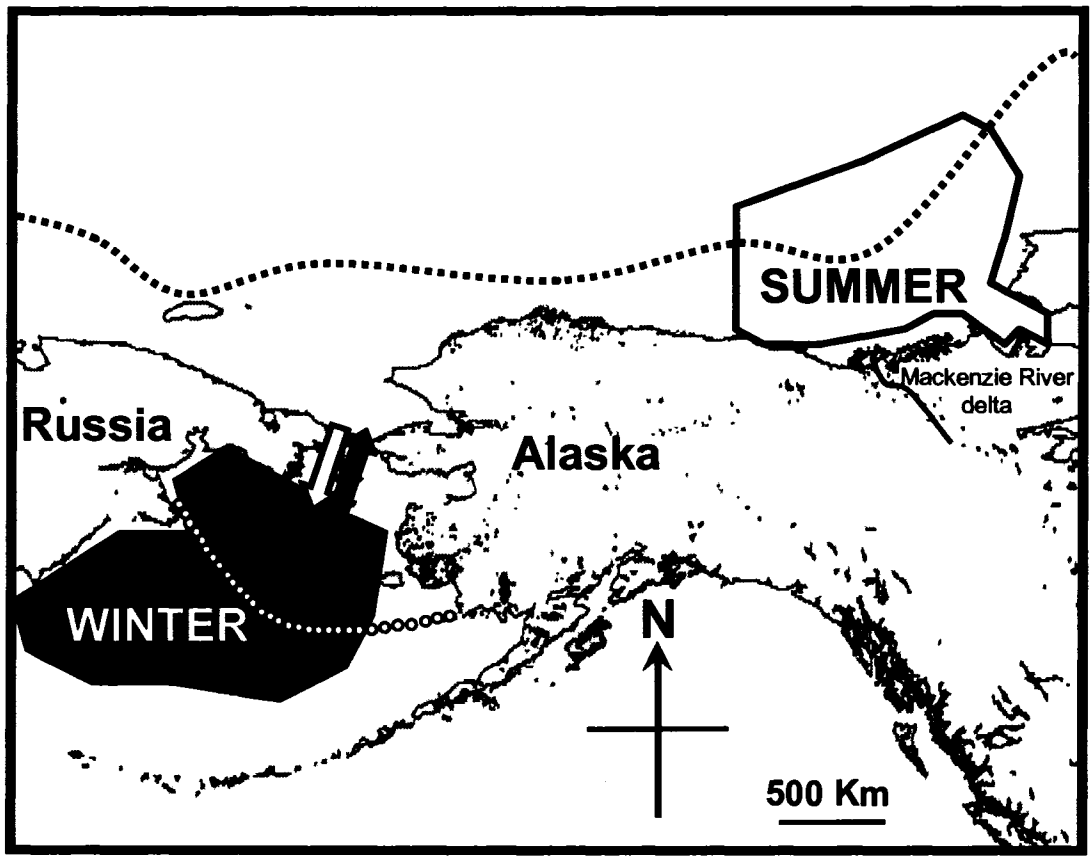

Figure 4.2. Migration pattern of western arctic bowhead whales (WABW). WABWs migrate north and east from the Bering Sea to the Beaufort Sea and Mackenzie river delta region (Dumont and Marion 1998). The curved white dashed line represents average winter sea ice extent in 2003 (according to the NOAA-Marine Modeling and Analysis Branch Reports; Picco 2005) and the black dotted line represents the mean arctic ice extent retreat (National Snow and Ice Data Center; http://www-nsidc.colorado.edu/data/).

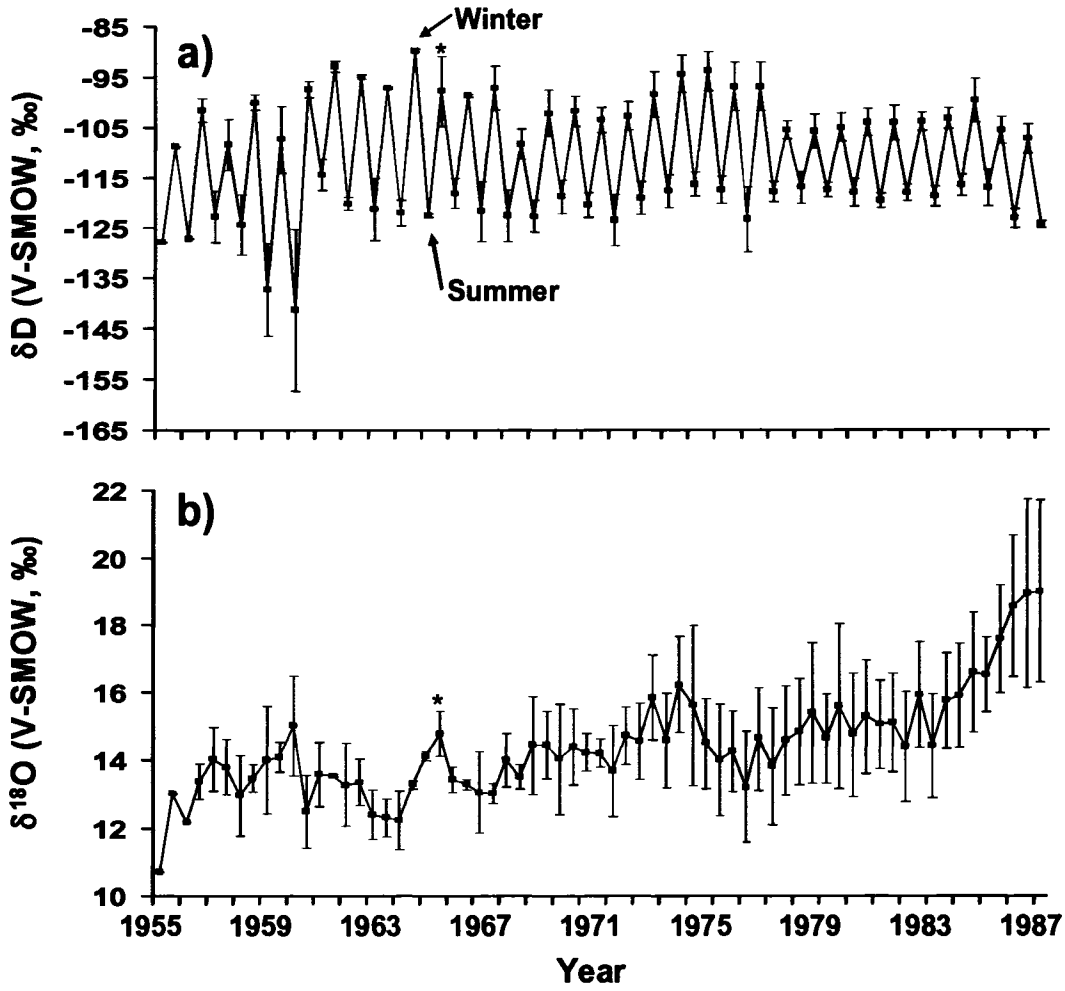

Figure 4.3. Mean δD (a) and $\delta^{18}O$ (b) values (‰, ± 1 SD) of WABWs for each year, with seasonal trend denoted in (a). Data represent all 14 whales analyzed in this study. Data before 1966 (*) and in 1988 (last two data points) was compiled from n = 2-5 whales, with all other points compiled from n = 6-10 whales.

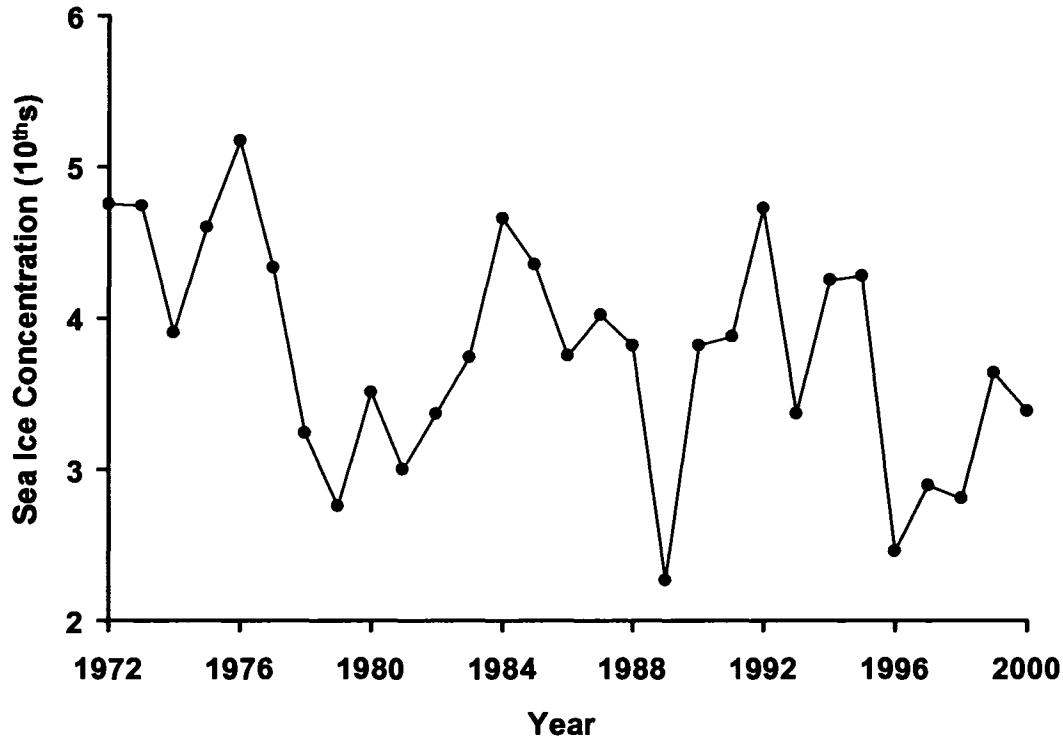

Figure 4.4. Sea ice concentration (10^{th}s) for each year from which satellite data are available.

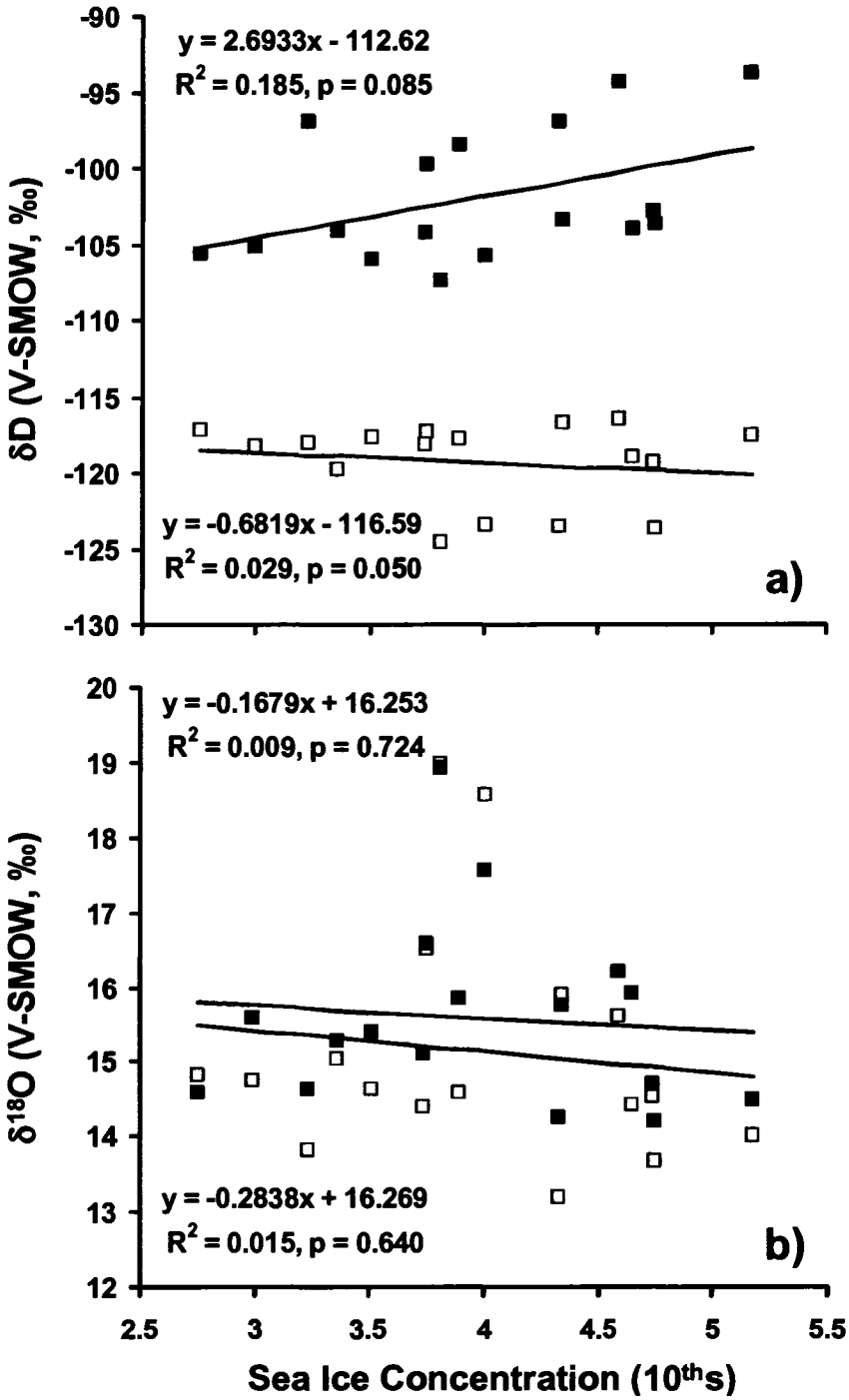

Figure 4.5. Mean WABW δD (a) and $\delta^{18}O$ (b) (‰) in winter (■) and summer (□) versus average sea ice concentration (Picco 2005) in the Bering Sea.

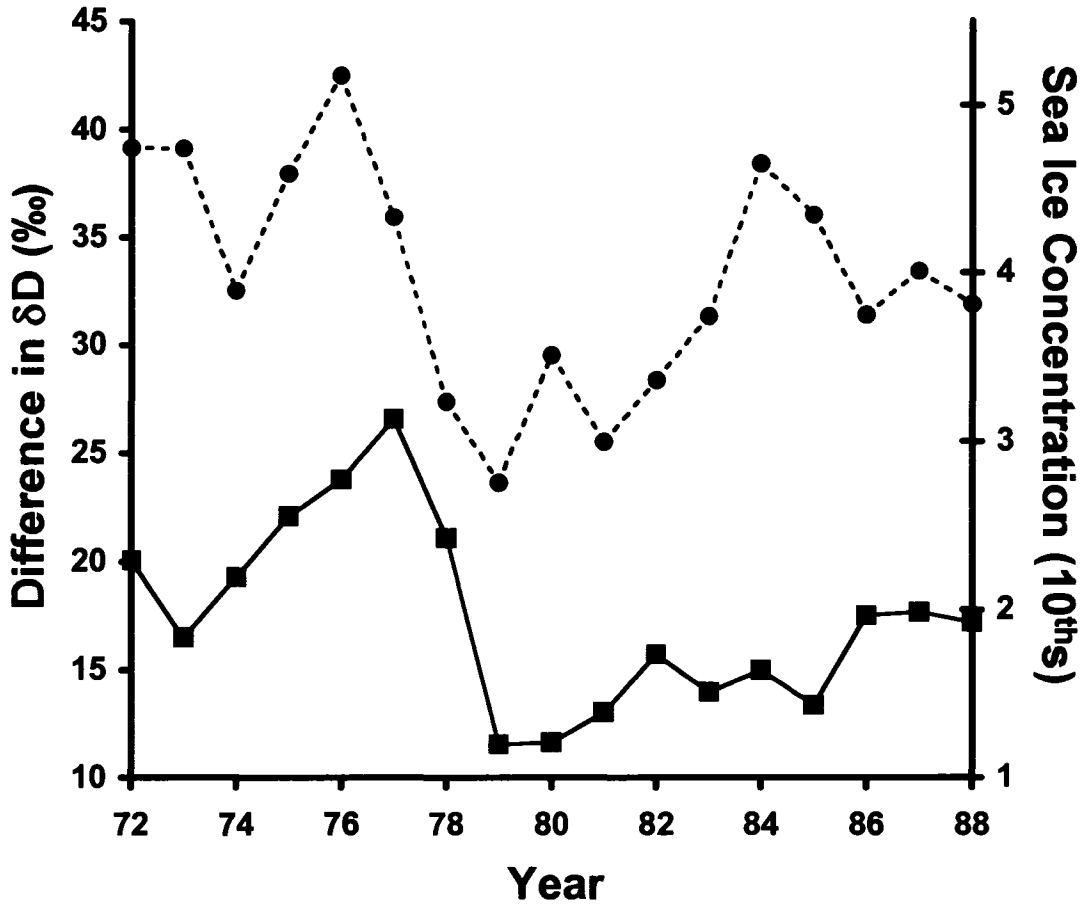

Figure 4.6. Difference in mean WABW δD (‰) between seasons (■), as well as corresponding sea ice concentration (●) plotted for each year.

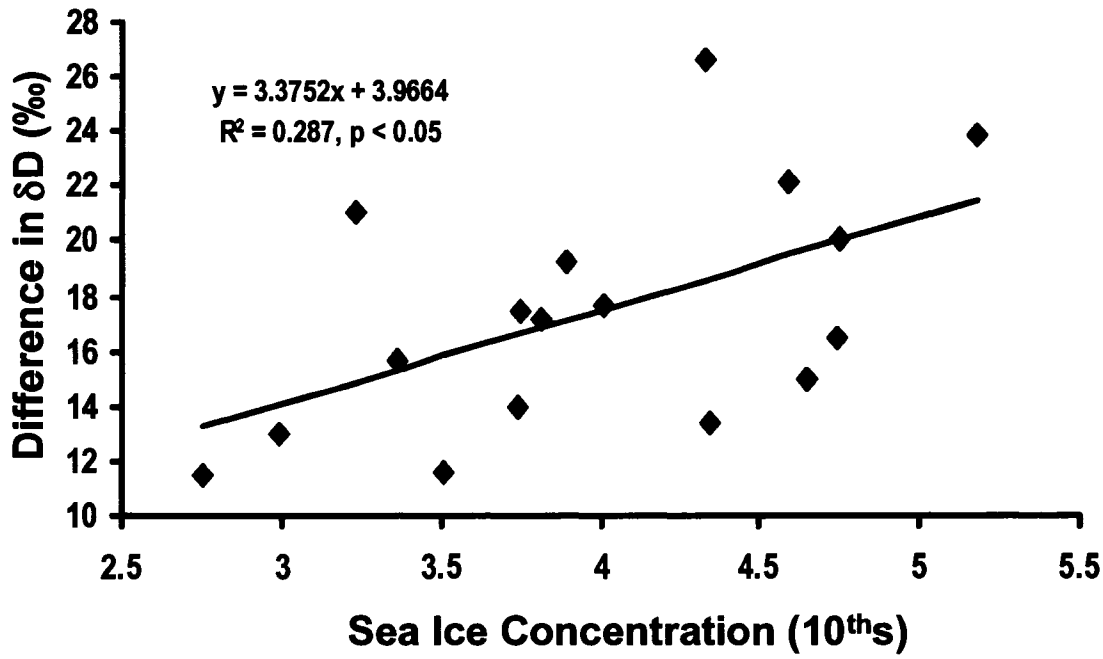

Figure 4.7. Difference in mean WABW δD (‰) versus yearly average sea ice concentrations (10^{th}s).

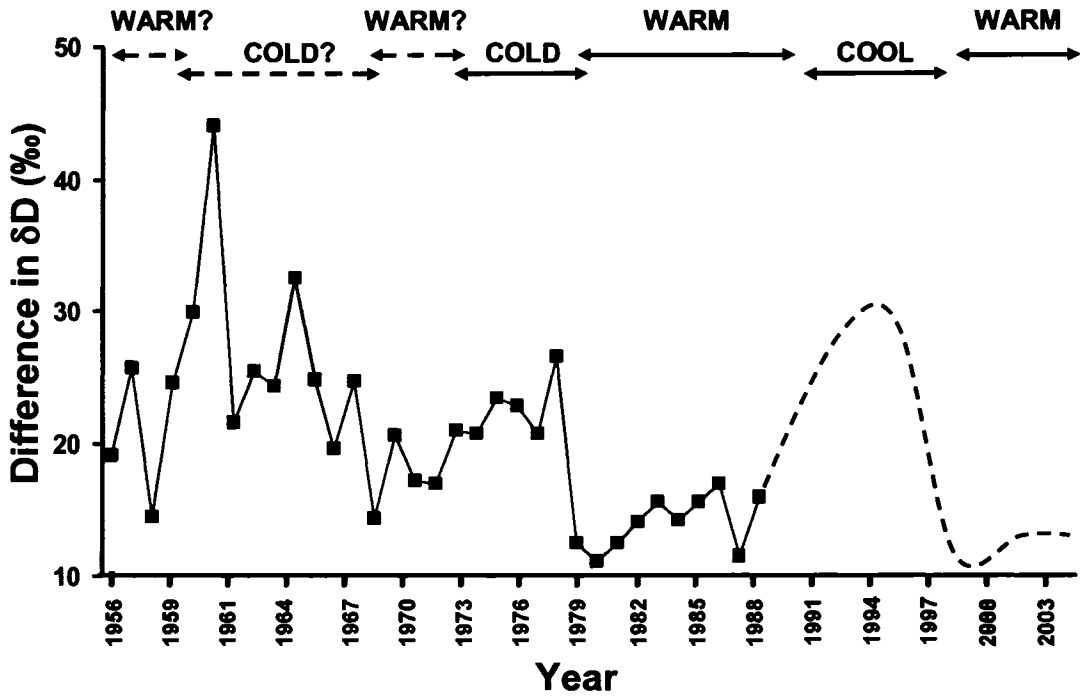

Figure 4.8. Difference in mean WABW δD (‰) between seasons (■), over the whole length of the temporal baleen record from 14 whales, with conceptual difference (dashed line) projected. Known (solid arrowed line) and proposed potential (dashed arrowed line) climate regime changes based upon analyses in this study.

Table 4.1. Mean $\delta^{18}O$ and δD values (‰) for bowhead whales for the Bering and Beaufort Seas, with listed p-values for the difference between the two regions for each isotope.

	Mean (± 1 SD)		p-value
	Bering	**Beaufort**	
$\delta^{18}O$	14.58 (1.45)	14.26 (1.59)	0.21
δD	-101.13 (5.03)	-121.65 (5.51)	<0.05*

CHAPTER 5

CONCLUSIONS

5.1. CONCLUSIONS

Global environmental change presents a growing challenge to scientists in all disciplines, and there is now paramount interest in gaining a more comprehensive understanding of the impacts these changes have on marine communities. This thesis contributes to the understanding of these multifaceted issues by using stable isotopes to track trends in animal ecology and related to environmental influences. Specifically, I have observed a change in the foraging ecology of Steller sea lions (SSL, *Eumetopias jubatus*) corresponding to a well-documented bottom-up driven regime shift in the North Pacific, outlined the utility of oxygen ($\delta^{18}O$) and hydrogen (δD) isotope analyses to examine migration patterns in bowhead whales (WABW, *Balaena mysticetus*), provided baseline values of trophic trends of $\delta^{18}O$ and δD in a marine ecosystem, and found a novel connection between WABW migration patterns and sea ice concentrations.

This study developed applications of stable isotope analyses to examine marine mammal ecology. First, with SSL, I demonstrated the consistency and utility of analyzing tooth samples to indicate fine-scale foraging patterns. By incorporating multiple years from individual animals, it was possible to assess temporal trends in individuals, and with a greater sample size on the population as a whole. By incorporating only tooth segments from SSL greater than two and a half years of age, no consistent ontogenetic trends between growth layer groups were detected. It is therefore likely that the higher isotopic

signature previously documented as evident in the early years of pre-weaned SSL was successfully avoided in this current study. While the values obtained from the teeth were similar to and in concordance with those expected from prior processing of whole bone samples in this thesis, each growth layer sectioned in the teeth of this study represent a range of years rather than a single data point in time. Finer sampling resolution could be performed in future studies to perfect the protocol, which could then yield increased temporal resolution. Tooth sampling in general leads to reconstruction of conceptual population and ecosystem patterns otherwise prohibited by opportunistic bone sampling. The 46-year SSL dataset, representing the years 1955-2001, and derived from samples taken across the entire range of the SSL, is the most comprehensive and subsequently representative to date. The results of this study reiterate that there may indeed have been some bottom-up driven influence on SSL foraging patterns, as animals likely fed in offshore regions more after the 1976 regime shift. Top-down ecosystem effects cannot be ruled out, however, as the shifts observed could be driven by either predation pressure on SSL or even due to fisheries pressure on available major prey items throughout their range in the nearshore regions. Future studies exploring the issue of marine mammal population declines in this region could consider that there indeed may have been a bottom-up trophic shift in the North Pacific over the past 40 years.

The utility of stable isotope applications was also explored in this thesis by analyzing the $\delta^{18}O$ and δD of whale baleen. As was originally the case with $\delta^{13}C$ and $\delta^{15}N$ of baleen plates, $\delta^{18}O$ and δD analyses provide a novel perspective of the annual migration of the WABW. The $\delta^{18}O$ and δD were found to vary along the length of the baleen, and

equivalent levels of variation were observed in the zooplankton. This study successfully furnished baseline $\delta^{18}O$ and δD values for multiple trophic levels of a marine ecosystem. Species-specific zooplankton separation showed closely paired patterns with regional water values, and there was a clear regional separation in the zooplankton between the winter (Bering Sea) and summer (eastern Beaufort Sea region) habitat of the whales in δD. Baleen samples not only confirmed the seasonal annual migration of the bowhead, but appeared to reflect the diet consumed in these two isotopically distinct regions. An unexpected result of this study was that the WABW and zooplankton were depleted in δD and enriched in $\delta^{18}O$ relative to the waters in which they reside. Further information and elucidation of this difference could result from examining the fine-scale patterns of fluctuation and amplitude variation in the isotopic data of both $\delta^{18}O$ and δD in an added layer of the ecosystem, the phytoplankton. Determination of minimum ages is also possible using $\delta^{18}O$ and δD by counting the number of annual cycles exhibited in the isotopic signals.

Given the life history characteristics of the bowhead whale, and the fact that this particular species spends much of its life associated with sea ice, the pairing of stable isotope trends in baleen and sea ice concentration data has proven to be an additional tool to both monitor the potential migratory behavior of bowhead whales in relation to environmental change. This method could serve as a proxy for reconstructing historical sea ice patterns. Given the observational gaps in historical environmental record (e.g., sea ice concentration), there is a clear need to develop long-term biological time series in the Arctic, as it is essential to document and interpret the effects of global warming on polar ecosystems. Examining δD patterns in historical WABW baleen and using them to reconstruct past

sea ice concentrations in the Bering Sea, Chukchi Sea, and Arctic Ocean could fit this need. More broadly speaking, the application of the techniques used in this study, particularly a multiple-isotope approach, could benefit investigations on trophic dynamics and the effects of global environmental change on aquatic and marine community structure.

Additional forms of evidence to support long-term changes in climate have been building rapidly, and it is clear that the observed warming in the Arctic in the past 100 years has no precedent since the early Holocene. Arctic and sub-arctic ecosystems will likely continue to change well into the future, and the degree to which animal populations can adapt to these changes remains unknown. For the continued preservation of biodiversity and ecosystem function, every effort should be made to continue the intense research on organismal adaptation and response to past environmental changes, in order to better quantify current patterns and predict future trends. As this study suggests, modern analytical techniques, such as stable isotope analyses, could further shed light on the impacts of environmental change to animal migratory and feeding ecology, and should be applied in multidisciplinary studies exploring these issues well into the future.

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